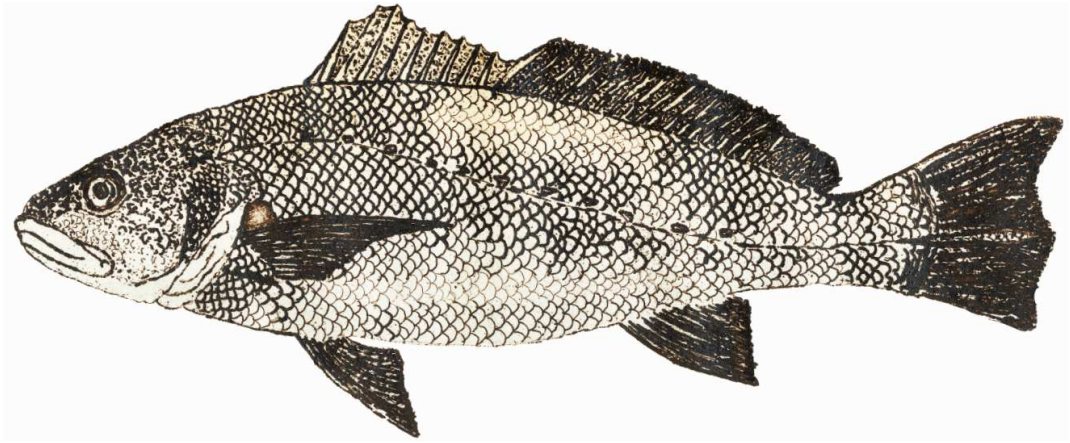
Comparisons of the biological and genetic characteristics of the Mulloway *Argyrosomus japonicus* (Sciaenidae) in different regions of Western Australia



This thesis is presented for the degree of
Doctor of Philosophy of Murdoch University

Submitted by

Bryn Morgan Farmer

BSc (Hons)

Murdoch University, Western Australia

2008

MURDOCH
UNIVERSITY
PERTH, WESTERN AUSTRALIA

Australian Government

Fisheries Research and
Development Corporation

Cover illustration taken from an intaglio and collagraph print by Carol Farmer

Declaration

I declare that this thesis is my own account of my research and contains as its main content work which has not previously been submitted for a degree at any university unless otherwise stated

……..

Bryn Morgan Farmer

2008

Abstract

The research conducted for this thesis has produced quantitative data on the biology and population genetics of the Mulloway *Argyrosomus japonicus* in Western Australia, where this sciaenid is recreationally and commercially fished. These data were used 1) to test various hypotheses regarding the relationship between key biological characteristics of *A. japonicus* and both latitude and environmental variables, 2) to investigate the population structure and genetic characteristics of populations of *A. japonicus* on the west and south coasts of Western Australia and to assess the relationships between these populations and those of *A. japonicus* in eastern Australia and South Africa and 3) to consider the implications of the biological and genetic results for management.

Argyrosomus japonicus was collected by angling and gill netting at intervals along the *ca* 1400 km of coastline between Carnarvon (24°53´S, 113°39´E) and Albany (35°01´S, 117°53´E). For the analyses, the distribution of this species was considered to comprise three main regions, 1) the upper west coast, *i.e.* Carnarvon to Kalbarri (27°42´S, 114°10´E), 2) the lower west coast, *i.e.* Kalbarri to Black Head (34°46´S, 115°57´E) and 3) the south coast, *i.e.* east of Black Head. All fish from the upper and lower west coasts, apart from those collected from the Swan River Estuary (32°04´S, 115°44´E), were obtained from nearshore and offshore marine waters, while those from the south coast were caught in an estuary, *i.e.* Oyster Harbour (34°58´S, 117°57´E). Fish were aged employing the number of opaque zones in sectioned otoliths, and population genetic structure was explored using nucleotide sequence variation in the control region of mitochondrial DNA.

Sampling of marine waters on the upper and lower west coasts yielded all stages of *A. japonicus* from small juveniles to large and old mature adults. The maximum total lengths and ages recorded for *A. japonicus* in marine waters on both the upper west coast (1293 mm and 25 years) and lower west coast (1437 mm and 32 years) were far greater than those recorded in the estuarine environment of Oyster Harbour on the south coast (813 mm and 10 years). It was not possible to obtain samples from marine waters on the south coast, where anglers encounter *A. japonicus* far less frequently than on the west coast, and consequently it was not possible to ascertain whether older fish were present in these waters.

The growth curves of female *A. japonicus* from the upper west and lower west coasts were not significantly different from each other and the same was also true for

the males from these locations ($p > 0.05$). The lengths at age of the females and the males on the whole of the west coast were thus pooled. Although the growth of females and males on the west coast were significantly different ($p < 0.05$), these differences were minor, as is illustrated by the small differences in their L_{∞}s, *i.e.* 1228 and 1189 mm, respectively, and *k*, *i.e.* 0.242 and 0.249 year $^{-1}$, respectively. Growth on the west coast was very rapid, with *ca* 80% of their asymptotic lengths being attained by females and males by only six years of life, at which age the majority of fish had already attained maturity. As the majority of fish on the south coast were ≤ 4 years old, comparisons between the growth on the west and south coasts were confined to those derived from the lengths at age of fish up to four years old. By age four, the fish on the west coast had attained *ca* 805 mm, whereas the females and males on the south coast had only reached *ca* 640 and 565 mm, respectively. Furthermore, at a given length, the fish on the west coast were relatively heavier than those on the south coast.

Argyrosomus japonicus spawned on the lower west coast between November and April, when the mean monthly water temperatures exceeded 19°C. On the other hand, spawning occurred throughout much or all of the year on the upper west coast, where the mean monthly water temperatures did not fall below 19°C. Although sampling was more restricted on the south coast, it provided evidence that spawning occurred at a similar time to that on the lower west coast. The collection in late spring/early summer of substantial numbers of the preflexion larvae of *A. japonicus* in plankton trawls in nearshore marine waters at 32°S on the west coast and the absence of the eggs/larvae of *A. japonicus* in catches obtained during extensive sampling for ichthyoplankton further offshore at a similar latitude, strongly indicate that this sciaenid spawns in nearshore waters.

Although *A. japonicus* typically spawns in nearshore coastal marine waters on the west coast, the following data collected for an assemblage in Mosman Bay in the lower reaches of the Swan River Estuary demonstrated that spawning also occurred in these estuarine waters: 1) *A. japonicus* was only caught and detected acoustically in Mosman Bay during the spawning period, *i.e.* late October to April. 2) All *A. japonicus* caught in Mosman Bay exceeded the L_{50} at first maturity and several of the females possessed stage VI ovaries, *i.e.* contained hydrated oocytes and/or post-ovulatory follicles. As Mosman Bay is essentially marine during late spring and summer, it provides environmental conditions analogous to those in protected coastal waters in which this species typically spawns. Since all females with stage VI ovaries were caught between 21:00 and 23:30 h, spawning must occur at night. Furthermore, as all of the

female fish with ovaries containing hydrated oocytes were caught immediately prior to the peak of high tide, there is a strong probability that the fertilised eggs would be transported downstream and out of the estuary on the ebb tide.

As the ovaries of mature females caught during the spawning period contained previtellogenic, cortical alveolar and yolk granule oocytes, and occasionally hydrated oocytes and/or post-ovulatory follicles, *A. japonicus* is an indeterminate spawner, *i.e.* fecundity is not determined prior to the onset of spawning.

The L_{50}s at first maturity of females on the lower and upper west coasts were not significantly different and the same was true for their males. The L_{50}s of females and males on the west coast were 903 and 880 mm, respectively, and far greater than the corresponding L_{50}s of 493 and 419 mm on the south coast. Furthermore, maturity was typically attained by females and males at an older age on the west coast, *i.e.* ≥ 5 years, than in Oyster Harbour on the south coast, *i.e.* ≤ 3 years.

On the west coast, juveniles, *i.e.* with lengths $< L_{50}$ at first maturity, were caught almost exclusively in nearshore waters < 10 m deep, whereas adults were caught in both those nearshore waters and in offshore waters, where depths ranged from 20 to 200 m. The small juveniles were found mainly in protected embayments and along low-energy beaches on the west coast and were abundant in the estuarine environment of Oyster Harbour on the south coast. The greater use of nearshore coastal waters as nursery habitats by *A. japonicus* on the west coast of Australia than is the case in eastern Australia and southern Africa is presumably related to a paucity of permanently-open estuaries and the presence of the protection provided to nearshore coastal waters by the chain of barrier reefs and islands that are found along this coast.

The spawning of *A. japonicus* over a far more protracted period on the upper west than lower west coast parallels the situation typically found in conspecific teleost populations at lower *vs* higher latitudes. However, the similarities in growth and length at maturity of *A. japonicus* on these two coasts contrasts with the differences frequently found between these variables in assemblages of the same species at different latitudes.

On the basis of the compositions of the mtDNA haplotypes of *A. japonicus*, it is concluded that the assemblages from Carnarvon on the upper west coast are genetically distinct from those of both Geraldton and Perth on the lower west coast, which are similar. However, the genetic composition of *A. japonicus* from the west coast overall differs markedly from that of this species in Oyster Harbour on the south coast. Thus, the assemblages of *A. japonicus* on the upper and lower west coasts represent different

populations (biological stocks) and these both differ, more markedly, from that found in Oyster Harbour on the south coast.

The genetic differences between the west coast and Oyster Harbour assemblages resided not only in haplotype composition but also in genetic diversity, with 11 to 14 haplotypes being detected in each of the three west coast locations compared with only one in that of Oyster Harbour. This indication that the latter assemblage has undergone substantial inbreeding is consistent with a substantial number of their individuals possessing deformities in their nasal olfactory openings and, to a lesser extent, their lower jaw, otoliths and operculum. As deformities were most common in 0+ and 1+ fish, those individuals may be particularly susceptible to mortality during the earliest years of life.

The mtDNA data for *A. japonicus* on the west coast of Australia were compared with corresponding but restricted data for populations in New South Wales and South Africa. These comparisons indicated that, while the genetic composition of *A. japonicus* on the west and east coasts of Australia were significantly different, the populations on those coasts had diverged relatively recently, and that the populations of *A. japonicus* in Australia and South Africa have been isolated for a much longer period and could potentially represent different species.

As the current minimum legal length for the retention of *A. japonicus* (MLL) in Western Australian waters is only 500 mm and thus well below the L_{50}s at first maturity of both the females (903 mm) and males (880 mm) of this species on the west coast, many fish on this coast will be caught and retained before they have had the opportunity to spawn. On the west coast, it would thus appear appropriate to consider a substantial increase in the MLL for this species, which is heavily fished in some of the nearshore waters typically occupied by the juveniles. As the spawning aggregations of *A. japonicus* in the lower reaches of the Swan River Estuary are targeted by the many recreational anglers that fish in this part of the estuary, managers may also need to provide this species with particular protection during the spawning period of this sciaenid in this estuarine region. Since the L_{50}s of female and male *A. japonicus* in Oyster Harbour were 493 and 419 mm, respectively, and thus below the current MLL of 500 mm, the majority of fish in this population would potentially have the opportunity to spawn at least once prior to being retained.

Table of Contents

Acknowledgements

I am indebted to a great number of people who have helped me throughout the course of my PhD. First and foremost, however, I would like to thank my supervisors, Professor Ian Potter, Professor Norm Hall and Doctor Jennie Chaplin, for giving me the opportunity to undertake this research at Murdoch University, providing direction and for sharing with me their collective wealth of knowledge on various aspects of fish biology and population genetics. The assistance provided by my supervisors was particularly telling towards the latter stages of writing-up and the many hours that were dedicated to answering questions and reading draft manuscripts was very much appreciated. This research was made possible through funding provided by the Fisheries Research and Development Corporation (FRDC) and Murdoch University.

Many people have helped with the collection of samples over the years and, in return, I hope to have provided some good fishing experiences. From Murdoch University's Centre for Fish and Fisheries Research (the infamous 'Fish Group'), Dan French, Alex Hesp, Peter Coulson, David Fairclough, Matt Pember, Tim Carter and Mike Travers have all helped at various times by line fishing for the often-elusive Mulloway. Thanks to Steeg Hoeksema and Ben Chuwen, whose extensive sampling on the south coast resulted in the discovery of a most interesting population of Mulloway. Thanks also to the aforementioned members of the 'Fish Group' and to Nicole Phillips, Glenn Moore and Ertug Sezmis for useful and stimulating discussion on various aspects of fish biology and data analysis. Finally, big thanks to all members of the 'Fish Group' who have made the last four years an enjoyable experience. Cheers guys!

While numbers of Mulloway were collected during fieldtrips, many more were obtained from commercial markets and I would particularly like to thank the guys at Geraldton Fish Market, Kai Fisheries in Carnarvon and Kailis Brothers in Canning Vale for providing samples and showing genuine interest in this research. The collective effort of the recreational angling community proved to be an invaluable source of further samples. There are a few recreational anglers that I would particularly like to thank, namely Jamie Waite, Allan Bevan, Anthony Simper and the guys at *Bluewater* (Melville), Ryan Thipthorp and the guys at *Oceanside Tackle and Marine*, Wally Parkin, Graeme Walker, Phil Hodgson and Graham Maunder. Big thanks also to *Western Angler*, *Hotbite* and *Fishing WA* magazines and particularly their respective editorial crews for the free advertising, which was instrumental in gaining the interest and support of Western Australia's recreational angling community.

I would also like to thank Rod Lenanton and Mark Cliff of the Western Australian Department of Fisheries for catch data and useful discussions on Mulloway. Thanks to the Western Australian Department of Fisheries and CSIRO for water temperature data. Cheers to Miles Parsons of Curtin University for sharing acoustic data and helping me to gain a greater understanding of the behaviour of Mulloway in the lower reaches of the Swan River. Arrie Klopper of the University of Pretoria kindly provided sequence data for South African *Argyrosomus japonicus* and useful discussions on genetics methodology. Veronica Silberschneider of New South Wales Fisheries, Matt Taylor of the University of New South Wales, and Greg Ferguson of SARDI Aquatic Sciences also provided interesting discussions on different aspects of Mulloway.

Last, but certainly not least, I would like to thank my friends and family for supporting me throughout the entire duration of this study. In particular, I would like to thank my Mum and Dad for always believing in me and supporting my decision to maintain my student lifestyle for as long as I have. Further thanks to Mum for the cover artwork and also to my brother for letting me know about all the good surf that I have missed out on while studying over the years. Cheers to Aaron Schoenberg, Dean Roberts, Josh Lewis, Chris Fenton, Michael Crake, and Aaron Dorai-Raj for their friendship and help with sample collection at various stages throughout the course of my PhD. I would finally like to thank Emma Sommerville for her support, particularly through the latter stages of writing-up and for helping me to relax and take my mind off Mulloway when I really needed to.

1.0 General introduction

1.1 The origin and evolution of the Sciaenidae

The Sciaenidae is a large family of perciform fishes which comprises at least 270 species that represent approximately 70 genera (Nelson, 2006; Froese and Pauly, 2007). The members of this family are distributed worldwide and are among the most common fishes in tropical and subtropical marine and brackish waters of the Atlantic, Pacific and Indian oceans (Trewavas, 1977; Chao, 1986), and have secondarily invaded fresh water in both North and South America (Chao, 1978). However, sciaenids are represented in freshwater by only six genera and 28 species, with these being predominantly restricted to the Atlantic drainages of South America (Chao, 1986; Casatti, 2003; Nelson, 2006).

Sciaenids possess a number of primitive characters (Sasaki, 1989; see also Section 1.2), which suggests that this family was derived early in the evolution of the Perciformes. Indeed, based on the distribution of monophyletic groups plotted on past geographic maps, it has been proposed that the Sciaenidae originated in the late Cretaceous or late Jurassic (Chao, 1986). While a late Jurassic origin provides the most parsimonious explanation and was thus supported by Chao (1986), this would predate the generally accepted late Cretaceous origin of the Perciformes (Greenwood *et al.*, 1966; McAllister, 1968; Lagler *et al.*, 1977). Furthermore, fossil sciaenids and particularly their otoliths have been most commonly found in the more recent Tertiary deposits that date back only to the Oligocene, *i.e.* 33.7-23.8 million years ago, and Miocene, *i.e.* 23.8-5.3 mya (Berg, 1958; Nolf, 1976a, 1976b; Monsch, 1998; Aguilera and Rodrigues de Aguilera, 2003). Although evidence from the fossil record largely supports a late Cretaceous origin, a fossil otolith from the prehistoric sciaenid *Otolithus bornholmiensis* was discovered in Denmark during the excavation of a deposit that is believed to predate the origin of the Perciformes (Malling and Grönwall, 1909; Chao, 1986). Thus, while a late Cretaceous origin appears most likely, there is some evidence that the origin of the Sciaenidae lies further back in prehistory.

Although the precise origins of the Sciaenidae remain unclear, so too does the relationship of the family with other percoid fishes. Based primarily on swimbladder and otolith morphology, it was initially proposed that the Sciaenidae was most closely related to the Haemulidae and Lutjanidae (Trewavas, 1977). Although Chao (1978) supported this hypothesis, he included, on the basis of the morphological descriptions of otoliths by Schmidt (1968) and Nolf (1976a, 1976b), the Sparidae with the other closely-related percoid families. Schwarzhans (1993) also concluded that the Haemulidae is the sister family to the Sciaenidae and provided as evidence the similarity between the sagittal otoliths of the extant genus *Pachyurus* and those of haemulids in general. Conversely, Sasaki (1989) has argued that most of the similarities between sciaenids and haemulids, as identified by Trewavas (1977), were pleisomorphies and produced evidence that the Haemulidae was the sister family of the Gerreidae. Sasaki (1989) provided further evidence for the monophyly of the Sciaenidae on the basis of 21 synapomorphies and the absence of relationships between this family and other families of the suborder Percoidei. However, Johnson (1993) has since demonstrated that five of the synapomorphies identified by Sasaki (1989) are shared with the Polynemidae (Fig. 1.1). These shared characteristics include similarities in two osteological characters, a sensory canal character and general larval morphology (Fig. 1.2; Johnson, 1993; Leis and Trnski, 2004). It was previously assumed that the polynemids were most closely related to the mugilids and sphyraenids due to their widely-separated dorsal fins (Nelson, 1984), but this relationship is no longer considered likely (Nelson, 2006). While recognising that further investigation was desirable, Johnson (1993) suggested that the Sciaenidae and Polynemidae should be included within a superfamily, Polynemoidea.

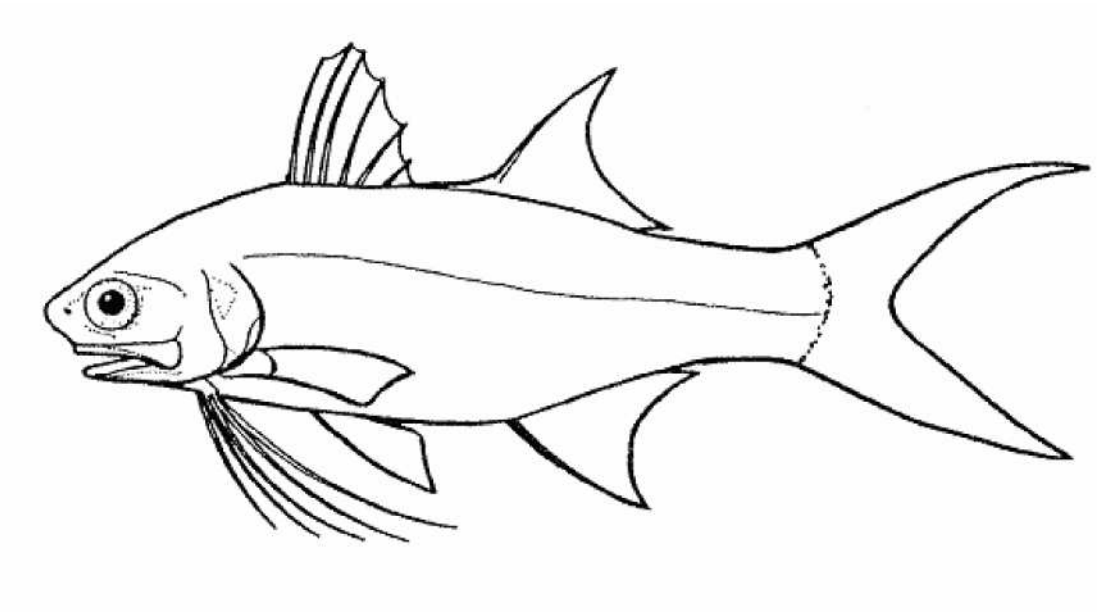


Figure 1.1. Stylised member of the Polynemidae, which has been proposed as a possible sister family to the Sciaenidae (Nelson, 2006).

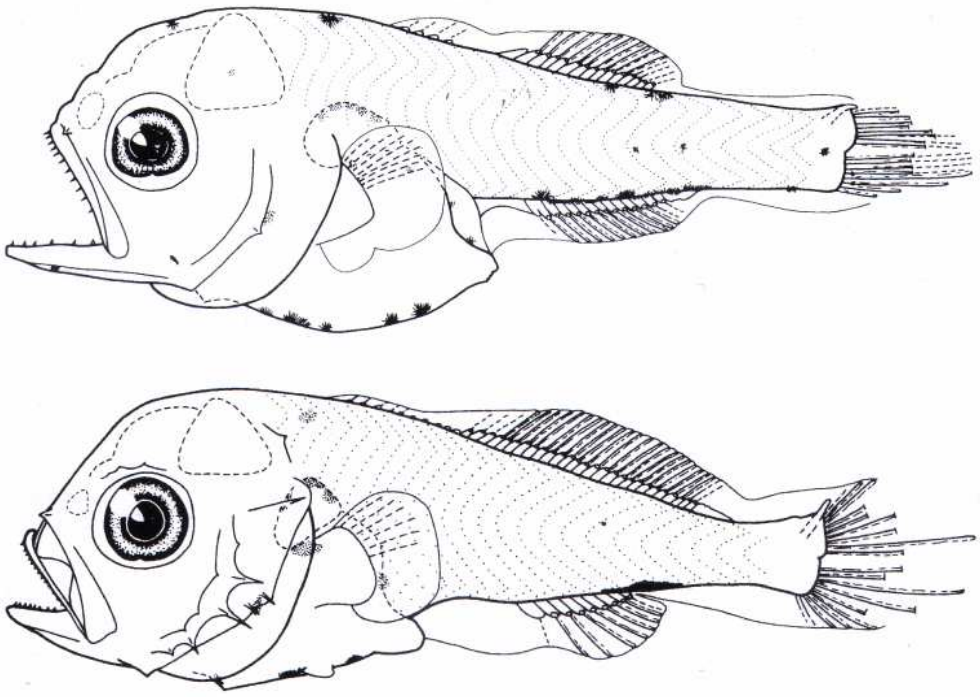


Figure 1.2. Larvae typical of the Polynemidae (top, 5 mm TL) and Sciaenidae (4.4 mm TL), which show many similarities despite members of each family having quite distinct adult forms (Leis and Trnski, 2004).

A recent study of the ultrastructure of the spermatozoa of six species of sciaenid and one species of polynemid has cast doubt on Johnson's (1993) hypothesis (Gusmão-Pompiani *et al*., 2005). Although the sciaenids analysed by Gusmão-Pompiani *et al*. (2005) share, with the polynemids, the same chromatin condensation pattern, type of midpiece and presence of short, irregular fins, they clearly differ in spermatozoa type, shape of the nucleus, position of the centrioles in relation both to the nucleus and to each other, centriolar stabilisation structures, length of the distal centriole and the shape and number of mitochondria. Furthermore, similarities among the spermatozoa of all sciaenids agree with the monophyly proposed for the family by Sasaki (1989), while also supporting the hypothesis that, in species of the same family, the sperm organelles have the same distribution (Baccetti *et al*., 1984; Burns *et al*., 1998; Abascal *et al*., 2002; Quagio-Grossiotto *et al*., 2003). Thus, while the theory of monophyletic origin is once again gaining momentum, the initial proposal of Chao (1978), namely that the Sciaenidae is most closely related to the Haemulidae, Lutjanidae and Sparidae, is also gathering support. For example, the phylogenetic relationship between these percoid families has been corroborated by the extant distribution of the dactylogyrid parasite *Euryhaliotrema* spp. (Boeger and Kritsky, 2003). However, according to the parasite data, the Sparidae is the sister group of the Sciaenidae, while both the Lutjanidae and Haemulidae comprise distinct basal lineages (Boeger and Kritsky, 2003).

1.2 Morphological characteristics and phylogeny of sciaenid fishes

The members of the Sciaenidae are morphologically very diverse, which reflects their very different feeding modes and life history patterns (Chao and Musick, 1977). In particular, there is a wide variety of body forms and mouth positions, which are reputed to be the most diverse of all percoid families (Chao, 1978). Equally as diverse is the maximum sizes attained by sciaenid fishes, which can range from only 100-300 mm for

representatives of the genus *Stellifer* to 1000-2000 mm for the relative "giants" of the genera *Argyrosomus*, *Bahaba*, *Cynoscion*, *Pogonias*, *Sciaenops* and *Totoaba*. Despite their great diversity in body form, two external characters, *i.e.* a continuous lateral line that extends to the caudal margin and an anal fin with one (less common) or two spine/s, are common to all sciaenids and distinguish them from all other percoid fishes (Chao, 1986; Fig. 1.3).

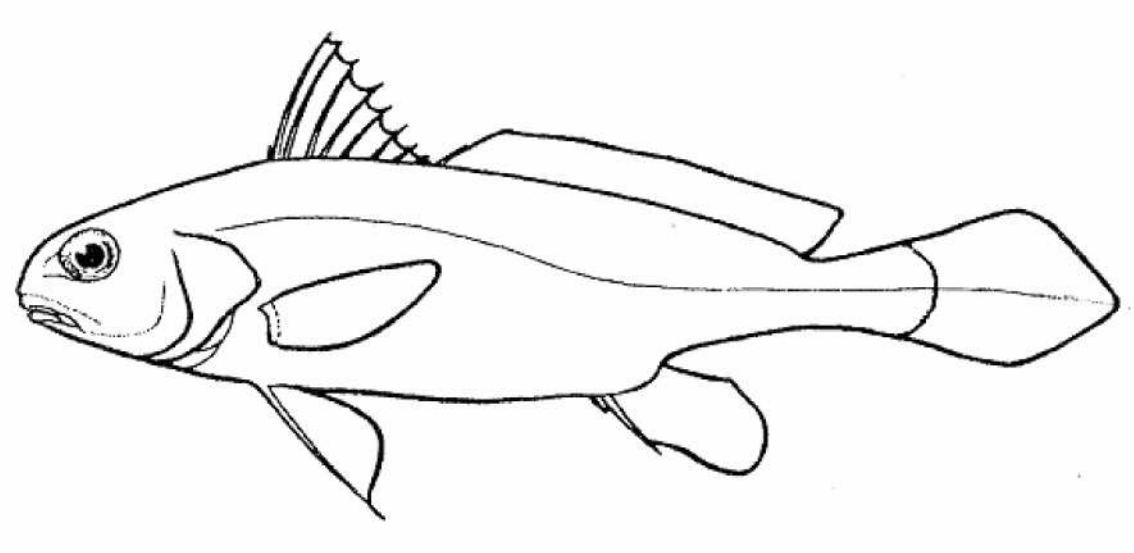


Figure 1.3. Stylised member of the Sciaenidae displaying some of the distinguishing characters of the family (modified from Nelson, 2006).

There are several additional characteristics that serve to unite the family (Trewavas, 1977; Nelson, 2006; Fig. 1.3). Their dorsal fin is long and, although the spinous portion, *i.e.* first dorsal, and soft portion, *i.e.* second dorsal, are usually separated by a deep notch, they are rarely completely separate; the first dorsal has between six and 13 spines, while the second dorsal has one spine and 20 to 35 rays; the caudal fin is slightly emarginate to rounded; the post-temporal bone has a fimbriate edge; the upper bony edge of the operculum is forked; teeth are usually absent from the vomer and palatine; some genera may have a single or a patch of small barbels on the

chin. However, the most characteristic feature of the Sciaenidae is probably its possession of specialised acoustic communication (Cruz and Lombarte, 2004).

The prevalence of acoustic communication amongst sciaenids may reflect adaptations to the turbid estuarine and nearshore coastal environments in which the members of this family are generally found (Trewavas, 1977; Chao, 1986; Blaber, 2000). Nevertheless, the ability of sciaenids to produce sound has long been known (Smith, 1905; Tower, 1908), and is reflected in the common English names for many representatives of the family, *i.e.* drums or croakers (Edgar, 2000; Nelson, 2006; Froese and Pauly, 2007). However, despite numerous studies of sciaenid sound production over more than a century, very little is known about the biological significance of these sounds (Ramcharitar *et al*., 2006). Many research workers have suggested that the sound produced by members of the Sciaenidae plays a role in reproductive behaviour (Guest and Lasswell, 1978; Takemura *et al.*, 1978; Mok and Gillmore, 1983; Saucier and Baltz, 1993; Connaughton and Taylor, 1995; Luczkovich *et al.*, 1999, 2000; Collins *et al.*, 2001; Ramcharitar *et al.*, 2001; Holt, 2002; Lagardère and Mariani, 2006; Ueng *et al*., 2007). However, since sciaenids generally aggregate to spawn and tend to do so in nearshore areas that are readily accessible to research workers, such as estuaries (*e.g.* Mok and Gillmore, 1983; Brown-Peterson *et al*., 2002; Macchi *et al.*, 2003), it is not surprising that studies of sound production have been largely undertaken during those times. Nevertheless, vocal communication certainly appears to play an integral role in the spawning behaviour of sciaenids, but the extent to which it is used throughout the remainder of their life history remains unclear.

The importance of acoustic stimuli to sciaenids is also reflected in the level of sophistication of those structures associated with sound production, *i.e.* sonic muscles and swim bladder, and sound detection, *i.e.* lateral line system and otoliths (Darovec, 1983; Chao, 1978, 1986; Gauldie, 1988; Helfman *et al*., 1997; Paxton, 2000; Lychakov

and Rebane, 2000, 2002; Cruz and Lombarte, 2004). Sciaenids exhibit a great diversity in both the variety of sounds produced and the mechanisms involved in their production and detection. This diversity in form has been used to determine taxonomic relationships within the family. The morphology of the swim bladder and sagittal otoliths, in particular, have been studied extensively and as this information is readily available for most sciaenids, it is these characters that have regularly been used to describe monophyletic groups worldwide (*e.g.* Chao, 1986). Comparative studies on osteology (Taniguchi, 1969a, 1969b, 1970; Sasaki, 1985) and facial musculature (Aguileira, 1982) have also demonstrated their importance in sciaenid phylogeny, but such data remain incomplete for many members (Chao, 1986), and are thus of limited use. Furthermore, while the lateral line system, pores and barbels on the snout and chin, scale sizes and arrangements, meristic counts and morphometric measurements are very useful for identifying taxa, they are limited as indicators of supra-generic relationships within the family (Chu *et al.*, 1963; Trewavas, 1964, 1977; Chao, 1978).

Despite having outlined a number of characters that have been used to distinguish members of the Sciaenidae, the close morphological similarities shared by many representatives has lead to the application of a range of taxonomic schemes that have been extensively revised over the years (*e.g.* Griffiths and Heemstra, 1995). Since molecular techniques are becoming much more rapid and cost-effective, they are being used increasingly to answer such taxonomic queries and have already proven useful for identifying cryptic species within a number of marine teleosts (Colborn *et al.*, 2001; Borsa, 2002). The genetic structure of many sciaenid species has also been determined using molecular techniques and a number of these have revealed the presence of substantial genetic divergence, without any accompanying morphological differences (Gold *et al*., 1993; Santos *et al*., 2003, 2006; Klopper, 2005).

1.3 The sciaenid fishes of Australian waters

In Australian waters, the Sciaenidae is represented by at least 17 species, encompassing nine genera, with the majority of these, *i.e. ca* 90%, being confined to the inshore waters of the continent's tropical north (Yearsley *et al*., 2006; Froese and Pauly, 2007; Table 1.1). The most speciose genera in northern Australian waters are *Johnius* and *Nibea*, which together are represented by a total of nine species (Sasaki, 1992; Yearsley *et al*., 2006; Table 1.1). As with most tropical Australian sciaenids, representatives of both of these genera are relatively small, *i.e.* with maximum total lengths < 650 mm, and are not heavily targeted by commercial or recreational fishers (Froese and Pauly, 2007). However, larger specimens of the River Jewfish *Johnius borneensis* and the Silver Jewfish *Nibea soldado* are retained opportunistically by fishers (Yearsley *et al*., 2001; Anon., 2007a). Another small sciaenid, the Silver Teraglin *Otolithes ruber*, is also caught opportunistically in the commercial and recreational fisheries of northern Australia (Yearsley *et al*., 2001; Anon., 2007a). Furthermore, since many of these tropical sciaenids occur in the same inshore habitat as the main commercially-targeted prawn species, they are often caught as bycatch during trawling operations (Blaber *et al*., 1990; Kennelly, 1995; Salini *et al*., 2001). While the majority of tropical Australian sciaenids are diminutive in size, the Black Jewfish *Protonibea diacanthus* is a notable exception. This sciaenid attains a maximum total length of *ca* 1500 mm and, owing to its large size and the palatability of its flesh, is commonly targeted by commercial and recreational fishers throughout its range in northern Australia (Phelan, 2002; Fletcher and Head, 2006).

In contrast to tropical Australian waters, those of the temperate south are relatively depauperate in terms of sciaenid diversity. In fact, there are only two members of the Sciaenidae, the Teraglin *Atractoscion aequidens* and the Mulloway *Argyrosomus japonicus*, which occur throughout the region (Trewavas, 1977; Kailola

Table 1.1. The sciaenid fishes of Australian waters. The division between tropical (above) and temperate (below) waters is shown by the dotted line, which extends offshore from just north of North West Cape (21º47'S, 114º09'E) in Western Australia and just north of Bundaberg (24º52'S, 152º21'E) in Queensland, and is based on the boundary between the tropical and transitional zones as outlined in the Interim Marine and Coastal Regionalisation of Australia (IMCRA 4.0; Commonwealth of Australia, 2006). Common names were allocated according to the most recent standard names of Australian fishes (Yearsley *et al.*, 2006).

Australian distribution	Scientific name	Common name
Tropical	*Atrobucca brevis*	Orange Jewfish
	Atrobucca nibe	Longmouth Jewfish
	Austronibea oedogenys	Yellowtail Jewfish
	Johnius amblycephalus	Bearded Jewfish
	Johnius australis	Little Jewfish
	Johnius borneensis	River Jewfish
	Johnius laevis	Smooth Jewfish
	Johnius novaeguinae	Paperhead Jewfish
	Larimichthys pamoides	Southern Yellow Jewfish
	Nibea leptolepis	Smallscale Jewfish
	Nibea microgenys	Smallmouth Jewfish
	Nibea soldado	Silver Jewfish
	Nibea squamosa	Scaly Jewfish
	Otolithes ruber	Silver Teraglin
	Protonibea diacanthus	Black Jewfish
		
Temperate	*Argyrosomus japonicus*	Mulloway
	Atractoscion aequidens	Teraglin

et al., 1993; Griffiths and Heemstra, 1995; Hutchins and Swainston, 2002; Table 1.1). Although *A. japonicus* occurs around the entire southern seaboard of Australia (see Section 1.4.1), *A. aequidens* is found exclusively in eastern Australia and primarily off the coast of New South Wales (Griffiths and Heemstra, 1995; Hutchins and Swainston, 2002). *Argyrosomus japonicus* is the largest Australian sciaenid, with a reported maximum length and weight of *ca* 2000 mm and *ca* 60 kg, respectively (Gomon *et al*., 1994; Hutchins and Swainston, 2002). However, reported estimates for the maximum size of *A. japonicus* in Australia are probably exaggerated due to their having taken into account the size of this species in southern Africa, where it attains a larger size (Griffiths and Heemstra, 1995; Heemstra and Heemstra, 2004). Nevertheless, the largest *A. japonicus* from Australian waters to have been weighed accurately was a 42.5 kg individual from Port Elliot in South Australia (Australian Anglers Association, National Fishing Records Database; www.aaawa.iinet.net.au/NationalAAAFishingRecords.html). The largest examples of *A. japonicus* reported in the Australian scientific literature include an individual of 34.7 kg that was caught near Dunsborough in Western Australia (Farmer *et al*., 2005), and an individual of 1690 mm that was caught in central New South Wales waters (Silberschneider and Gray, 2005). *Atractoscion aequidens* also grows to a relatively large size, with a reported maximum length of *ca* 1200 mm and weight of *ca* 20 kg (Kailola *et al*., 1993; Griffiths and Hecht, 1995b; Griffiths and Heemstra, 1995; Yearsley *et al*., 2001). However, this species also attains a larger size in southern African waters and the largest *A. aequidens* on record in Australia is 9 kg (Heemstra and Heemstra, 2004; Australian Anglers Association, National Fishing Records Database).

1.4 *Argyrosomus japonicus*

1.4.1 Distribution and habitats

Argyrosomus japonicus has been reported from four geographically-isolated regions of the Indian and Pacific Oceans that are bound approximately by the latitudes of 20º and 40º, both north and south of the equator (Fig. 1.4). In the Northern Hemisphere, *A. japonicus* occurs along the coast of Pakistan into north-west India and along the Chinese coast from Hong Kong to southern Korea and Japan (Trewavas, 1977; Griffiths and Heemstra, 1995; Fig. 1.4). In the Southern Hemisphere, this species is distributed along the entire southern seaboard of Australia, from Bundaberg in southern Queensland to North West Cape in Western Australia, and along the east coast of southern Africa, from the Cape of Good Hope to southern Mozambique (Trewavas, 1977; Kailola *et al*., 1993; Griffiths and Heemstra, 1995; Fig. 1.4).

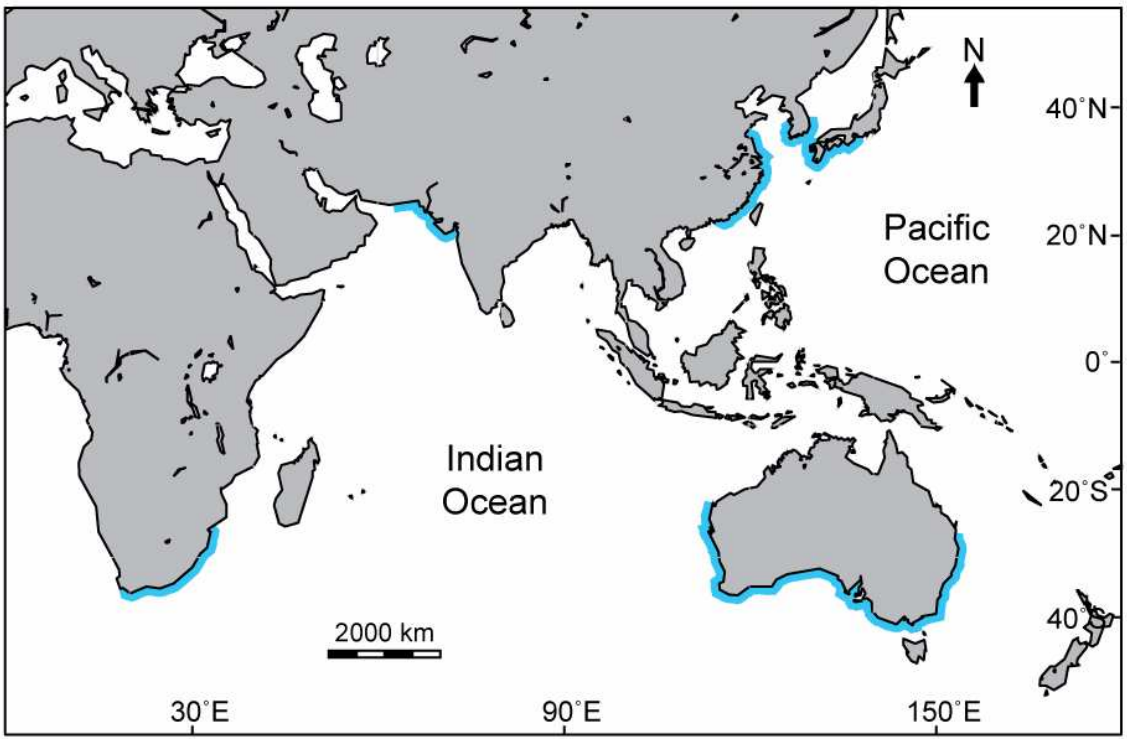


Figure 1.4. The documented worldwide occurrence of *Argyrosomus japonicus*.

The two Northern Hemisphere regions within which *A. japonicus* is reported to occur are separated by a geographical barrier in the form of the Indian landmass, which extends into equatorial waters and past the apparent physiological limit of their distribution, *i.e.* 20º N. This distributional limit may be maintained due to the eggs and larvae of *A. japonicus* not being able to survive water temperatures that exceed 30ºC (Battaglene and Talbot, 1994), a temperature that is regularly reached in equatorial waters (NOAA; www.osdpd.noaa.gov/PSB/EPS/SST/sst_anal_fields.html). In the Southern Hemisphere, the vast expanse of the Indian Ocean between the African and Australian continents serves to isolate populations. Since *A. japonicus* has not been encountered in waters deeper than *ca* 200 m in either of these continents (Kailola *et al*., 1993; Griffiths and Heemstra, 1995; B. Farmer, pers. obs.), the depth of the Indian Ocean presumably acts as a physical boundary to adult migration. Furthermore, since *A. japonicus* spawns in the nearshore coastal waters of both continents and its larvae exhibit a rapid transition to a demersal stage (Griffiths, 1996; Smith, 2003; see Chapter 4), the expanse of the Indian Ocean would also act as a barrier to the advection of eggs and larvae.

Wherever it occurs, *Argyrosomus japonicus* exploits a diverse range of coastal habitats, which include the lower reaches of rivers, estuaries, protected embayments, exposed ocean beaches, areas around reef structures in both nearshore and offshore waters, and is found down to depths of at least 200 m (Kailola *et al.*, 1993; Griffiths and Heemstra, 1995; Griffiths, 1996; B. Farmer, pers. obs.). However, the relative utilisation of each of these habitats differs with life history stage and also by season. The juveniles of *A. japonicus* are thus found exclusively in nearshore waters (Hall, 1986; Griffiths and Heemstra, 1995; Griffiths, 1996; Silberschneider and Gray, 2005), while the highly migratory adults move between all of the habitats listed above, but are more likely to be in nearshore environments from late spring to early autumn (Anon., 1993; Griffiths,

1996; Cusack and Roennfeldt, 2002; Farmer *et al*., 2005). The extent to which these habitats are utilised, and particularly of the various nearshore environments by the juveniles, also differ with geographical location. For example, juvenile *A. japonicus* enter estuaries in far larger numbers in New South Wales and southern Africa than on the lower west coast of Australia (Griffiths, 1996; Silberschneider and Gray, 2005; see Chapter 4), where they appear to use nearshore coastal waters to a greater extent as nursery habitats.

1.4.2 A confused taxonomy

The lack of clear morphological differences amongst members of the genus *Argyrosomus* has lead to the application of a range of taxonomic schemes that have been extensively revised over the years (*e.g.* Griffiths and Heemstra, 1995). In fact, *Argyrosomus japonicus* has been known by at least 13 different synonyms and, until 1995, had most recently been referred to as *A. hololepidotus* in both South Africa and Australia (Lin, 1940; Trewavas, 1977; Griffiths and Heemstra, 1995). In the latest revision of the genus (Griffiths and Heemstra, 1995), South African, Australian and Japanese populations of *A. japonicus* could not be separated on the basis of morphological or meristic characteristics and were thus considered a single species. However, given the geographical isolation of these populations, the marked differences in the maximum lengths and ages recorded for this sciaenid in South Africa and Australia, and the results of comparisons of mitochondrial DNA sequences for both South African and Australian individuals (Klopper, 2005; see also Chapter 5), further subdivision of this apparent species complex seems inevitable.

Despite the revision in scientific nomenclature (Griffiths and Heemstra, 1995), *A. hololepidotus* has continued to be used by some workers for Australian members of this species (*e.g.* Fletcher and Head, 2006; Yearsley *et al.*, 2006). However,

A. hololepidotus is endemic only to its type locality of Madagascar and is a very different sciaenid to *A. japonicus* (Griffiths and Heemstra, 1995). Furthermore, given the lack of published genetic data to suggest that South African and Australian *A. japonicus* are distinct from those of Japan, *i.e.* the type locality for this species (Temminck and Schlegel, 1843), the revised scientific nomenclature of *Argyrosomus japonicus*, as proposed by Griffiths and Heemstra (1995), has thus been used throughout this thesis. This also follows the account of the Sciaenidae in the Fishes section of the Zoological Catalogue of Australia (Hoese *et al*., 2006).

1.4.3 Commercial fisheries in Australia

Argyrosomus japonicus is caught recreationally and commercially throughout its entire range in Australian waters, being commonly targeted in Western Australia, South Australia, Victoria, New South Wales and Queensland. Although *A. japonicus* is caught on the west coast of Victoria and in southern Queensland, it is most abundant in Western Australia, South Australia and New South Wales, which is reflected in the commercial and recreational catches reported from those states (Kailola *et al*., 1993). The commercial catch of *A. japonicus* has been reliably reported from 1940 for New South Wales (Silberschneider and Gray, 2005) and from 1950 for South Australia (Hall, 1986; Ferguson and Ward, 2003). While commercial catch data have been reported by species since *ca* 1962 in Western Australia (Australian Bureau of Statistics, Western Australian Fisheries Production Bulletin), the early records are incomplete and thus reliable catch data for Western Australia are available only from 1975 (Western Australian Department of Fisheries, commercial catch database).

In New South Wales, the majority of the commercial catch of *A. japonicus* comes from estuaries, with 65% of the catch during 2003/2004 being taken in these systems (Silberschneider and Gray, 2005). The estuarine catches are predominantly

obtained by setting gill nets in the deeper estuaries that experience high freshwater flows, such as those of the Hawkesbury, Clarence and Shoalhaven Rivers (Silberschneider and Gray, 2005). Catches of *A. japonicus* in the Hawkesbury River are thus greatest during periods of increased freshwater discharge (Anon., 2003). While *A. japonicus* is caught predominantly in the estuarine fisheries in this state, small numbers of this species are also taken by hook and line in marine waters. Between 1940 and 1970, the reported total annual commercial catch of *A. japonicus* in New South Wales fluctuated between 50 and 100 tonnes (Silberschneider and Gray, 2005). After 1970, when otter trawling in coastal waters increased and the minimum legal length for retention was removed, annual commercial landings of *A. japonicus* increased sharply to peak at 380 tonnes in 1973/74 (Silberschneider and Gray, 2005). Subsequently, the annual catch of *A. japonicus* in New South Wales has steadily declined to a minimum of 60 tonnes in 2003/04 (Silberschneider and Gray, 2005). However, since the catch per unit effort (CPUE) has remained relatively stable during this period (Silberschneider and Gray, 2005), the decrease in catches may, at least partly, reflect a reduction in the number of fishers targeting *A. japonicus* in New South Wales. As well as being caught in a number of target fisheries in New South Wales waters, *A. japonicus* also form a significant component of the discarded bycatch from estuarine and oceanic prawn trawls (Gray *et al*., 1990; Broadhurst and Kennelly, 1994, 1995; Liggins and Kennelly, 1996; Liggins *et al*., 1996; Kennelly *et al*., 1998; West and Walford, 2000).

As in New South Wales, the commercial catch of *A. japonicus* in South Australia comes primarily from estuaries, with at least 80% of the catch being taken from the Coorong Lagoons (Hall, 1986; Ferguson and Ward, 2003). The remaining 20% of the commercial catch of *A. japonicus* is taken from coastal waters immediately adjacent to the Coorong and the marine waters of Gulf Saint Vincent and the far west coast (Hall, 1986; Ferguson and Ward, 2003). Catches of *A. japonicus* from the marine

waters outside the Coorong come predominantly from the shark gill net fishery (Hall, 1986). Within the Coorong, *A. japonicus* is caught using gill nets and beach seine nets, while those in coastal waters are caught using not only those same methods, but also hook and line (Hall, 1986; Ferguson and Ward, 2003). The annual commercial catch of *A. japonicus* in this state in the years 1950 to 2002 fluctuated between 30 and 215 tonnes (Hall, 1986; Ferguson and Ward, 2003). After remaining stable at *ca* 40-60 tonnes, the catch of *A. japonicus* has increased in recent years (Ferguson and Ward, 2003). As with catches of *A. japonicus* in the Hawkesbury River in New South Wales, the catch rate of *A. japonicus* in the large mesh gill net fishery in the Coorong Lagoons and swinger net fishery of the Younghusband Peninsula are both positively correlated with freshwater discharge from the Murray River (Hall, 1984, 1986; Ferguson and Ward, 2003).

Unlike the situation in New South Wales and South Australia, the majority of the commercial catch of *A. japonicus* in Western Australia comes from coastal and offshore waters rather than estuaries (Fletcher and Head, 2006). In Western Australia, *A. japonicus* are caught mostly by hook and line in the Shark Bay snapper fishery and the shark gill net fisheries of the west and south coasts (Fletcher and Head, 2006). A very small percentage of the annual commercial catch of *A. japonicus* also comes from estuarine fisheries, such as those based in the Swan River and a number of south coast estuaries (Smith, 2006; Smith *et al*., 2006). The average annual catch of *A. japonicus* from the Swan River between 1995 and 2004 was only 173 kg, and the numbers caught in south coast estuarine fisheries in 2004/05 was so low that they did not even rate a mention (Smith *et al*., 2006). While the current estuarine fisheries do not contribute greatly to the commercial catch of *A. japonicus* in Western Australia, the fishery based on this species in the lower reaches of the Swan River Estuary used to be more substantial. However, unlike the eastern states estuarine fisheries, which are based

largely on the juveniles of *A. japonicus*, this fishery targeted mainly adult fish, *i.e.* with total lengths of at least one metre (Riggert, 1978; Cusack, 2004). The commercial catches of *A. japonicus* from the Swan River Estuary have been reported since 1912, with the annual catch up to 1974 averaging 1.5 tonnes (Riggert, 1978). While commercial fishing for *A. japonicus* in the Swan River has declined in recent years, these records indicate a long history of fishing in this system.

Despite a reduction in commercial fishing in the Swan River, the seasonal aggregations of adult *A. japonicus* in the lower reaches of this system have become an increasingly popular target for recreational anglers and the catches taken by this sector now exceed that of the commercial fishery (Malseed and Sumner, 2001; Smith, 2006; see Section 1.4.4). The total annual catch of *A. japonicus* by all commercial sources in Western Australia has fluctuated between *ca* 10 and 75 tonnes since 1975, with the peak of *ca* 75 tonnes being landed in 2001/02 (Western Australian Department of Fisheries, commercial catch database). Since this peak, the annual reported commercial catch of *A. japonicus* in this state declined to *ca* 58 tonnes in 2002/03, *ca* 34 tonnes in 2003/04, *ca* 28 tonnes in 2004/05 and *ca* 27 tonnes in 2005/06 (Western Australian Department of Fisheries, commercial catch database). However, since the catch per unit effort (CPUE) has only decreased by a small amount during this time (Western Australian Department of Fisheries, commercial catch database), reductions in total annual catch may also partly be due to a reduction in the number of fishers targeting *A. japonicus* in Western Australia.

1.4.4 Recreational fisheries in Australia

Since *Argyrosomus japonicus* attains a large size and seasonally exploits a range of habitats that are readily accessible by shore or boat, this sciaenid is highly sought-after by recreational fishers in Australian waters (Kailola *et al*., 1993; Cusack and

Roennfeldt, 2002; Henry and Lyle, 2003). While anglers using rod and line are responsible for the majority of *A. japonicus* caught, fish are also occasionally taken in gill nets or speared by snorkellers (Kailola *et al*., 1993). Despite securing a reputation as a particularly enigmatic species, experienced recreational anglers, who have gained a good knowledge of the seasonal movements of *A. japonicus*, can target them all year round. In fact, the recreational effort directed at catching *A. japonicus* in some Australian states is so high that the catches by this sector can far outweigh those taken by their respective commercial fisheries.

Estimates of the total recreational catch in Australian waters has been determined only for 2001, in which year it was estimated that *ca* 323 000 *A. japonicus* were retained and a further 276 000 were released (Henry and Lyle, 2003). The estimated total weight of *A. japonicus* retained in Australian waters during this year was *ca* 925 tonnes, with the majority of fish in terms of weight being caught in New South Wales, *i.e. ca* 274 tonnes, and Western Australia, *i.e. ca* 360 tonnes (Henry and Lyle, 2003). These estimates are far higher than those for *A. japonicus* retained by the commercial fishers of either of these states during 2001, which were *ca* 74 tonnes in New South Wales and *ca* 75 tonnes in Western Australia (Penn, 2003; Silberschneider and Gray, 2005). It is important to recognise, however, that a small number of other sciaenids, such as the Black Jewfish *Protonibea diacanthus*, were probably included in those data for recreational anglers in Western Australia.

In New South Wales, recreational anglers catch *A. japonicus* predominantly in the larger permanently-open estuaries (Wilson, 2004). In fact, in terms of weight, *A. japonicus* ranked in the top ten fish caught in northern New South Wales estuaries (West and Gordon, 1994; Gartside *et al*., 1999), compared with eleventh by weight and twentieth by number during an earlier survey of recreational fishers in Botany Bay (Anon., 1981). *Argyrosomus japonicus* is less frequently encountered by recreational

anglers in coastal and offshore waters, with the species ranking as low as fifteenth by weight and fortieth by number in estimates of the total catches of recreational offshore trailer boat anglers during a survey by Steffe *et al*. (1996). Similarly, the majority of the South Australian recreational catch of *A. japonicus* is taken from estuarine waters and particularly from the Coorong Lagoons (Ferguson and Ward, 2003). Recreational gill netting, as well as line fishing, is allowed in the Coorong and catches consist predominantly of juvenile fish (Ferguson and Ward, 2003). Smaller numbers of *A. japonicus* are also taken from coastal waters immediately adjacent to the Coorong, but these catches tend to include much larger individuals (Ferguson and Ward, 2003).

In Western Australia, recreational anglers obtain *A. japonicus* predominantly from nearshore coastal waters and particularly the protected marine embayments and surf beaches of the mid-west coast, *i.e.* from Geraldton at 28°47'S, 114°37'E to Carnarvon at 24°53'S, 113° 39'E. This sciaenid is also caught in the lower reaches of south-western Australian estuaries, and particularly those of the Swan and Kalgan rivers. While recreational anglers commonly catch *A. japonicus* in both of these systems, the two estuaries differ markedly in their fishery characteristics. For example, while it is rare to encounter *A. japonicus* with total lengths less than one metre in the Swan River (Cusack and Roennfeldt, 2002; B. Farmer, pers. obs.), the Kalgan River recreational fishery is based primarily on smaller fish with total lengths of 400 to 600 mm (B. Farmer, pers. obs.). Furthermore, while *A. japonicus* are actively targeted and usually retained in the Swan River, those caught in the Kalgan River are generally taken as incidental by-catch by anglers targeting the Black Bream *Acanthopagrus butcheri* and are usually released. An increasing number of recreational anglers are also now targeting the aggregations of *A. japonicus* that form seasonally in depths of *ca* 100 m in the offshore waters of Perth (A. Bevan, Shikari Charters, pers. comm.).

1.4.5 Management regulations in Australian fisheries

Argyrosomus japonicus is regularly caught in the commercial and recreational fisheries of five Australian states, *i.e.* Western Australia, South Australia, Victoria, New South Wales and Queensland. The majority of the fisheries for *A. japonicus* are managed by spatial and temporal fishing restrictions, gear regulations, minimum legal lengths for retention (MLLs) and recreational bag limits that can vary markedly between state jurisdictions. In Queensland, New South Wales and Victoria, the commercial and recreational fisheries that are based on *A. japonicus* are managed uniformly statewide and their MLLs are detailed in Table 1.2, along with their respective daily recreational bag limits. Since *A. japonicus* is managed on a regional basis in South Australia and the management of this species in Western Australia is of particular relevance to this study, the current fishing regulations for each of these states are discussed in more detail below.

In South Australia, fishing for *A. japonicus* is managed in two distinct regions; within the Coorong Lagoons and in all marine waters outside of the Coorong. *Argyrosomus japonicus* are plentiful within the Coorong Lagoons, but the majority of these fish have total lengths between 450 and 650 mm (Ferguson and Ward, 2003). Presumably, it is the abundance of these small fish, together with the presence of a long established commercial fishery, that has lead South Australian Fisheries managers to allow *A. japonicus* to be taken by commercial and recreational fishers at a smaller total length in the Coorong, *i.e.* 460 mm, than in all other marine waters, *i.e.* 750 mm (Table 1.2). The daily recreational bag limits of the two regions also differ, with 10 fish being allowed to be retained from the Coorong in any 24 h period and only two fish allowed from all other marine waters. However, only two fish in the allowable bag of 10 from the Coorong can have a total length > 750 mm TL.

Since Western Australia encompasses such a wide latitudinal range, within which the species composition and fishing pressure varies, commercial and recreational fishing is managed within four broad biological regions; the Pilbara/ Kimberley, Gascoyne, West Coast and South Coast (Fletcher and Head, 2006). While *Argyrosomus japonicus* is commonly encountered in all but the former of these regions, the regulations regarding the retention of *A. japonicus* remain unchanged throughout. In both commercial and recreational fisheries, *A. japonicus* must have a total length of at least 500 mm to be retained, while the recreational bag limit allows two fish to be kept during any 24-hour period commencing at midnight (Table 1.2).

Table 1.2. Minimum legal lengths (MLL) for the retention of *A. japonicus* in the commercial and recreational fisheries and daily recreational bag limits in all states of Australia that the species is caught. * These bag limits can include only two fish with total lengths > 750 mm. NA, not applicable.

State	Management regions	MLL	Recreational bag limit
Qld	NA	450 mm	10
NSW	NA	450 mm	5*
Vic	NA	500 mm	10
SA	Within Coorong	460 mm	10*
	All other waters	750 mm	2
WA	Gascoyne, west coast and south coast	500 mm	2

The MLLs and recreational bag limits for *A. japonicus* vary between state jurisdictions and few of these were based on biological criteria. However, a notable exception is in the South Australian marine waters outside the Coorong, where the size limit for *A. japonicus* has been set according to the size at maturity (L_{50}) as determined for the species by Hall (1986). In theory, ensuring that the harvesting of individual

A. japonicus occurs above the size at maturity should help provide adequate protection for the spawning stock/s of this species and thus enhance the level of recruitment into the fishery. However, it should be noted that commercial and recreational fishers are allowed to take *A. japonicus* at a far smaller length than that of maturity in what appears to be a major nursery area for the species in South Australia, *i.e.* the Coorong Lagoons.

1.5 Fishery and conservation considerations for sciaenid fishes

It is widely assumed that highly fecund fish species are particularly resilient to fishing and the threat of biological extinction (Mace and Hudson, 1999; Roberts and Hawkins, 1999; Hutchings, 2001; Sadovy, 2001). The Sciaenidae is one such family of highly fecund fishes and its members form a significant component of the catches of commercial and recreational fisheries throughout the tropical and subtropical oceans of the world (Chao, 1986; Froese and Pauly, 2007). The larger species in this family, *i.e.* with maximum total lengths greater than one metre, are particularly sought after and at least two of these, including the Chinese Bahaba *Bahaba taipingensis* and the Totoaba *Totoaba macdonaldi*, are critically endangered and under serious threat of extinction (Sadovy and Cheung, 2003). These two sciaenids are among the largest representatives of the family, with both attaining maximum total lengths of *ca* 2000 mm and weights in excess of 100 kg (Flanagan and Hendrickson, 1976; Trewavas, 1977; Figs 1.5, 1.6). *Bahaba taipingensis* and *T. macdonaldi* both have very limited geographical distributions, with the former sciaenid only occurring in Chinese waters from the Yangtze River southwards to Hong Kong (Trewavas, 1977; Sasaki, 2000), while the latter is endemic only to the Gulf of California (Cisneros-Mata *et al*., 1995). As is typical of many sciaenids, these species aggregate in large numbers and migrate into nearshore waters during the spawning season (Flanagan and Hendrickson, 1976; Cisneros-Mata *et al*., 1995; Sadovy and Cheung, 2003). While fishers now locate

Figure 1.5. The largest known fresh specimen of *Bahaba taipingensis*, caught as by-catch while trawling outside Castle Peak Bay, western Hong Kong (Photo: Mr Cheng Tai-sing).

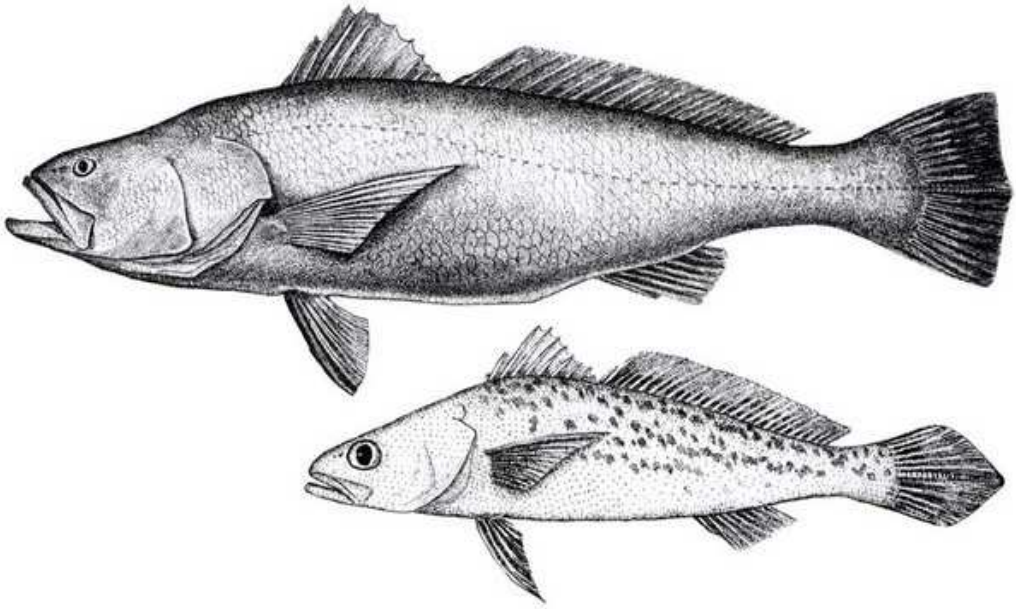


Figure 1.6. Adult and juvenile of the Totoaba *Totoaba macdonaldi* (picture: A. Kerstitch).

schools using passive sonar gear, the conspicuous drumming sounds made by these sciaenids enable fishers to locate aggregations simply by listening for sounds transmitted through the hulls of their boats (Sadovy and Cheung, 2003).

The dramatic reduction in the stocks of both of the above species arose primarily due to increased fishing pressure as a result of their high market values, palatable meat and highly esteemed swim bladders (Cisneros-Mata *et al*., 1995; Sadovy and Cheung, 2003). The swim bladders of large sciaenids are particularly sought after in China, where they are appreciated for their putative medicinal properties, such as in the prevention of miscarriages and as a general tonic for health (Lin, 1939; Sadovy and Cheung, 2003; Courchamp *et al*., 2006). As the numbers of *B. taipingensis* plummeted in Chinese waters, swim bladder prices increased so markedly that the price per unit weight eventually exceeded that of gold by seven times (Sadovy and Cheung, 2003). The high commercial value of the swim bladders of *B. taipingensis* prompted fishers to continue their efforts, even at very low fish densities and, by 2001, some 70 years after it was first reported in the scientific literature, *B. taipingensis* was virtually extinct (Dulvy *et al*., 2003). The steady reduction in numbers of *B. taipingensis* in Chinese waters during the late 1970s led to an increased demand for swim bladders of the imported *T. macdonaldi* (Cisneros-Mata *et al*., 1995). However, while aggregations of adult *T. macdonaldi* were being increasingly targeted to supply the Chinese market, the juveniles were also being caught as by-catch in a rapidly proliferating commercial shrimp fishery in the Gulf of California (Cisneros-Mata *et al*., 1995). Thus, in the case of *T. macdonaldi*, it was high juvenile mortality as well as heavy exploitation of adult spawning aggregations that lead to their demise. Both *B. taipingensis* and *T. macdonaldi* are now listed as 'critically endangered' on the IUCN Red List of Threatened Species (www.iucnredlist.org). In addition, both sciaenids are now under protective legislation throughout their limited distributions, while *T. macdonaldi* has also been listed in

Appendix I of the Convention on International Trade in Endangered Species (CITES) (Barrera-Guevara, 1990).

The examples of *Bahaba taipingensis* and *Totoaba macdonaldi* illustrate that neither high fecundity nor increasing rarity necessarily protects marine fishes from critical depletions and the potential threat of extinction. In fact, the human predisposition to place exaggerated value on rarity fuels disproportionate exploitation of rare species, rendering them even rarer and thus more desirable, ultimately leading them into what has been termed an 'extinction vortex' (Courchamp *et al*, 2006). While the case studies of *B. taipingensis* and *T. macdonaldi* have been the most publicised, similar patterns of overexploitation are a common feature of large sciaenids throughout the world. While some members of the family have disappeared from large areas of their historical geographic distribution, others have been fished to very low levels throughout their range. For example, *Argyrosomus regius* is no longer caught in the Wadden Sea in the Netherlands (Wolff, 2000a, 2000b), while *Protonibea diacanthus* has all but disappeared from Hong Kong waters (James, 1994). Also in Chinese and Hong Kong waters, the commercial catch of the sciaenids *Pseudosciaena crocea, Pseudosciaena polyactis* and *Atrobucca nibe* is greatly reduced (Kawasaki, 1987; Pitcher *et al*., 1998). Furthermore, stocks of *Argyrosomus japonicus* on the east coast of southern Africa are recruitment overfished and greatly depleted throughout their range (Griffiths, 1996, 1997b). Clearly, the suite of biological, ecological and fishery characteristics that typify many members of the Sciaenidae make them especially vulnerable to exploitation. Thus, given this inherent vulnerability and our limited understanding of many exploited species within this family, closer attention to their monitoring and management has been urged (Sadovy and Cheung, 2003).

1.6 General aim

Baseline biological data, such as those on age compositions, growth rates and reproductive biology, are required for the development of appropriate management policies aimed at conserving any commercially or recreationally exploited fish species. More recently, molecular approaches have been used to help discriminate between stocks and to detect cryptic species, the results of which may require unique management strategies. Since the *A. japonicus* that occur in each of the four geographically-isolated regions outlined earlier in this chapter may be newly-recognised endemic species, this means that any management decisions based on biological data obtained, for example, for *A. japonicus* in South Africa may be inappropriate and unlikely to provide this species with the protection that it requires throughout much of its range. The concern over stocks of similarly large sciaenids elsewhere in the world, including *A. japonicus* in southern Africa and the congeneric *A. regius* in Europe, highlights the requirement for a more detailed knowledge of *A. japonicus* in Australian waters. The collection of those biological data that are required to ensure the rational management of the commercial and recreational fisheries that are currently based on *A. japonicus* in Western Australian waters was thus the primary aim of this study. However, since the distribution of *A. japonicus* in Western Australia covers such a wide latitudinal range, encompassing a wide variety of environmental conditions, these data were also used to explore the ways in which the biological characteristics of *A. japonicus* varies by geographical location in this state. More specific aims are provided in the Introductions to each of the data Chapters 3-5.

2.0 Study regions, sampling regime and general methods

2.1 Study regions

Argyrosomus japonicus was collected from a number of locations along the approximately 1400 km stretch of the south-western Australian coastline between Carnarvon (24°53´S, 113°39´E) and Albany (35°01´S, 117°53´E) (Fig. 2.1). For the purposes of this study, and based on boundaries outlined in the Integrated Marine and Coastal Regionalisation of Australia (IMCRA 4.0; Commonwealth of Australia, 2006), this stretch was divided into the upper west, lower west and south coasts (Fig. 2.1).

2.1.1 Upper west coast

The upper west coast extends from Quobba (24°30´S, 113°24´E) in the north to Kalbarri (27°42´S, 114°10´E) in the south (Fig. 2.1) and, under IMCRA, encompasses the Zuytdorp and Shark Bay bioregions (Commonwealth of Australia, 2006). The upper west coast is semi-arid to arid and, due to the low annual rainfall, contains only three major rivers, *i.e.* the Gascoyne, Wooramel and Murchison (Brearley, 2005; Commonwealth of Australia, 2006). While the Murchison River is perennial, the Gascoyne and Wooramel rivers are seasonal and dry out along much of their length (Brearley, 2005).

Although the continental shelf along the upper west coast is relatively wide, this region is characterised by a typically heavy swell. Cliffs and narrow intertidal platforms are a feature of the exposed western coasts, while the gulf regions of Shark Bay and the nearshore waters of Carnarvon offer a more sheltered environment with tidal sand flats and lagoons. The marine environment off the exposed western coast includes extensive areas of sublittoral rocky reefs (Commonwealth of Australia, 2006), while sand substrate, often with small patches of rocky reef and rubble, is a feature of the more sheltered environments (Anon., 1996). Hypersaline regions are also a feature of Shark Bay, particularly in the southern part of its eastern gulf (Logan and Cebulski, 1970;

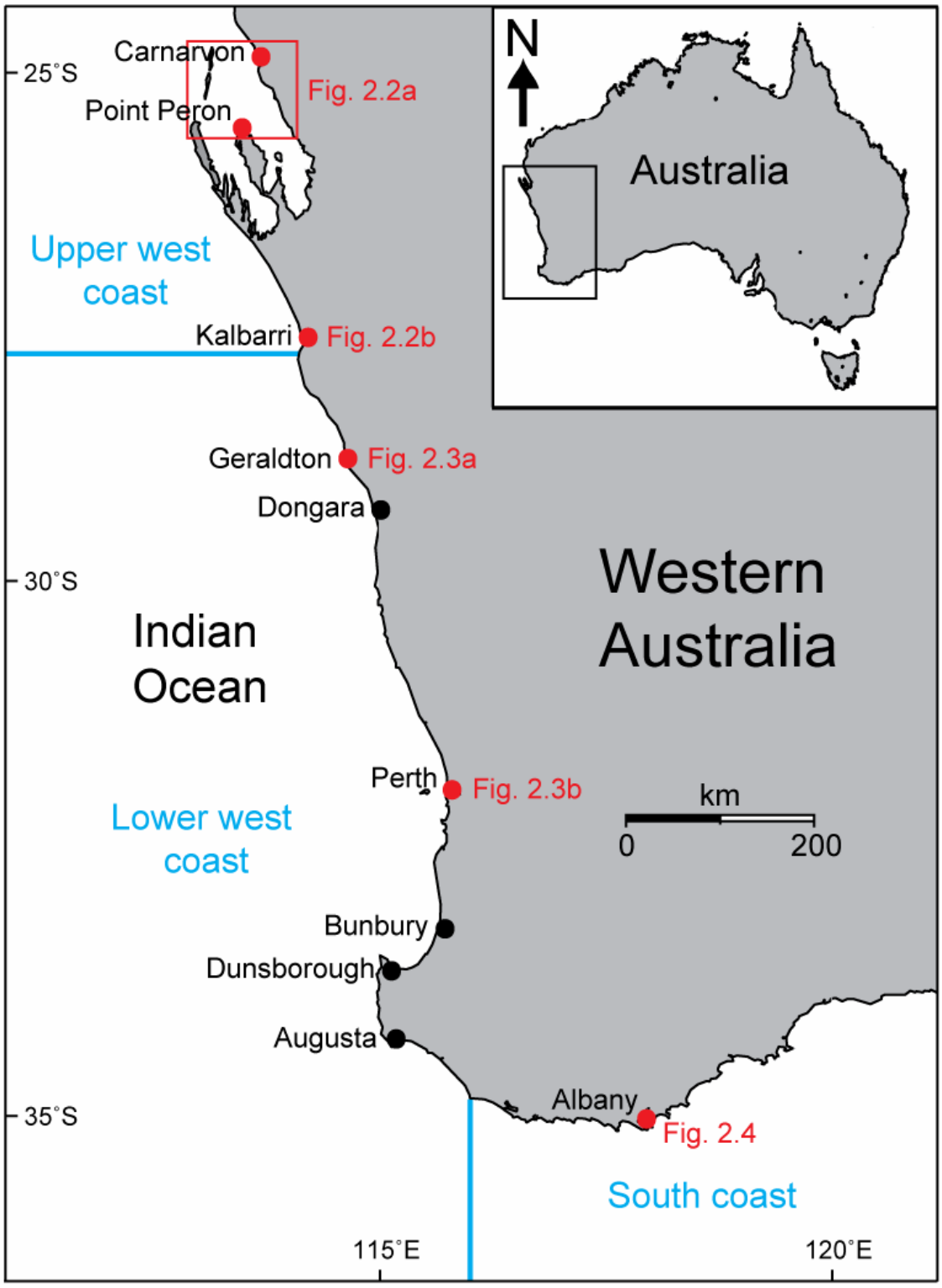


Figure 2.1. Map showing the locations along the south-western Australian coast from which samples of *Argyrosomus japonicus* were collected. Solid blue lines indicate the boundaries between the upper west, lower west and south coasts. The solid red circles denote the localities from which the majority of samples were obtained and which are shown in greater detail in Figures 2.2-2.4.

Burling *et al*., 2003). While the waters of the upper west coast are influenced greatly by the southwards-flowing Leeuwin Current, which flows strongest from autumn to winter (Godfrey and Ridgway, 1985; Gersbach *et al*., 1999; Woo *et al*., 2006), there are also significant inshore currents in this region. As the inshore currents of the upper west coast are predominantly wind-driven, their direction and rate of flow depends largely on the seasonal patterns of wind (*e.g.* Gersbach *et al*., 1999; Pearce and Pattiaratchi, 1999). Strong south-westerly winds occur along the upper west coast between October and March, which in turn drive the inshore and northwards flowing Capes and Ningaloo Currents (Gersbach *et al*., 1999; Pearce and Pattiaratchi, 1999; Taylor and Pearce, 1999; Woo *et al*., 2006). At other times, winds on the west coast are variable or light to moderate west and the net current flow is southwards (Taylor and Pearce, 1999).

Although Shark Bay lies within a transition zone between tropical and temperate environments, the majority of the fauna found in this embayment have a tropical affinity (Wells, 1980; Wilson and Allen, 1987; Black *et al.*, 1990; Hutchins, 1990; Jones, 1990; Slack-Smith, 1990; Anon., 1996; Pember, 1999; Travers, 1999). The dominance of tropical fauna in Shark Bay is attributable to the southwards transport of the larvae of tropical species by the Leeuwin Current, which flows relatively close to this coast during the autumn and winter (Legeckis and Cresswell, 1981; Hutchins, 1990; Jones, 1990; Slack-Smith, 1990). Seagrass meadows provide a very important habitat in Shark Bay, covering an area of *ca* 4000 km^2 and comprising 12 species (Walker, 1990). They contain both temperate species, *e.g. Amphibolis antarctica* and *Posidonia australis*, and tropical species, *e.g. Syringodium isoetifolium* and *Halophila deciphens*, (Walker, 1990; Huisman, 2000). While Shark Bay does not contain any true coral reefs, it houses 80 species of hermatypic coral, which are prominent in the more sheltered waters around Bernier, Dorre and Dirk Hartog Islands (Marsh, 1990). Various species of algae are also common on the rocky reefs within the eastern and western gulfs of Shark Bay

(Commonwealth of Australia, 2006). Although the marine biota of the Kalbarri area has not been thoroughly studied, the sparse information that is available suggests that the rocky shore intertidal faunas comprise a mixture of tropical, *i.e.* Indo-West Pacific, west coast endemic and temperate species (Commonwealth of Australia, 2006). Nearshore sublittoral rocky reefs are covered with algae, but these communities are also relatively unstudied.

On the upper west coast, *A. japonicus* was collected from Carnarvon/Shark Bay and Kalbarri (Figs 2.1, 2.2a/b). In Carnarvon/Shark Bay, this species was obtained from the nearshore waters of Carnarvon, the offshore waters on the mainland side of Bernier and Dorre Islands, *i.e.* Carnarvon Basin, and from Point Peron (Fig. 2.2a). The nearshore waters of Carnarvon that were sampled constituted the beach immediately adjacent to the township, which is characterised by a predominantly sandy substrate, and Miaboolya Beach, which is a sheltered coastal beach situated to the north of Carnarvon that contains significant mangrove habitat (Aylmore and Anderson, 2003). Miaboolya Beach is a major nursery area for the juveniles of many fish species, including *A. japonicus*, and has been designated a Fish Habitat Protection Area by the Western Australian Department of Fisheries (Aylmore and Anderson, 2003). The offshore waters sampled were in Carnarvon Basin, which remains < 16 m deep throughout and contains a variety of habitats, *i.e.* seagrass, coral and unvegetated sand (Seddon, 1972; Anon., 1996). The Point Peron sampling site, which was relatively shallow, *i.e.* <3 m depth, was characterised by rocky rubble over a sand substrate. In Kalbarri, *A. japonicus* were caught 1) at Oyster Reef, which is characterised by patchy reef substrate, 2) in the surf zone north of the mouth of the Murchison River, which is characterised by intertidal reef platforms interspersed by long sandy beaches, and 3) in an area of sublittoral rocky reef *ca* 1 km offshore from Blueholes (Fig 2.2b).

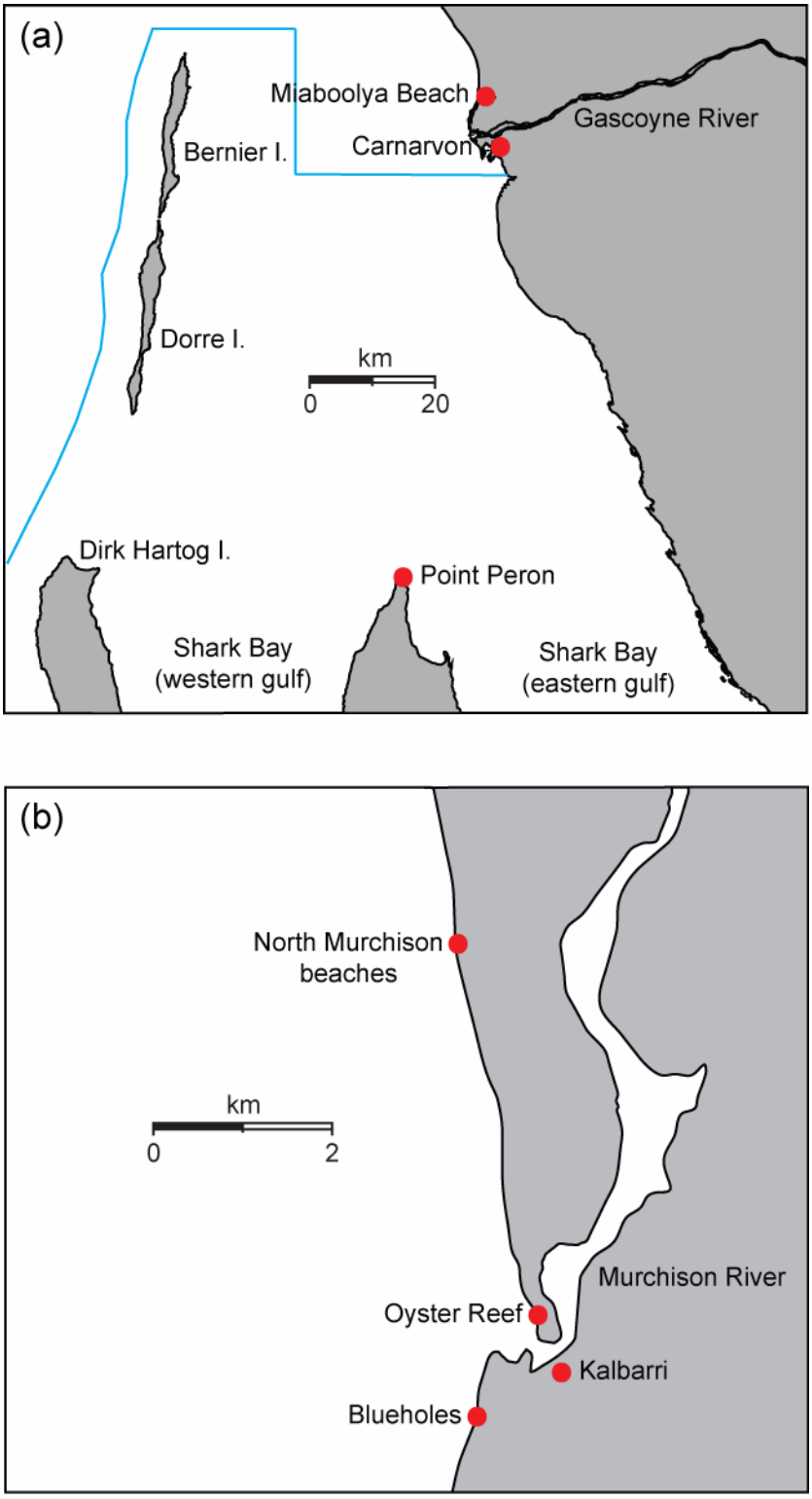


Figure 2.2. Map showing the main sampling locations for *Argyrosomus japonicus* on the upper west coast of Western Australia. These were located in (a) Carnarvon/Shark Bay and (b) Kalbarri. The solid blue line in (a) shows the boundary of the Shark Bay World Heritage Area.

2.1.2 Lower west coast

The lower west coast extends southwards from Kalbarri, around the capes, *i.e.* Naturaliste and Leeuwin, and eastwards to Black Head (34°46´S, 115°57´E) (Fig. 2.1). Under IMCRA, this portion of coast encompasses the Central West Coast and Leeuwin-Naturaliste bioregions (Commonwealth of Australia, 2006). The lower west coast is characterised by a temperate climate, receiving moderate rainfall and possessing several small rivers and estuaries throughout (Brearley, 2005). Several of the estuaries along this coast are either seasonally-open, intermittently-open or normally-closed, as the entrances are usually closed when river flow is low (Lenanton and Hodgkin, 1985; Hodgkin and Hesp, 1998; Brearley, 2005). Furthermore, some of these estuaries, such as the Hutt, Bowes, Oakabella, Oakajee and Buller, may dry out completely in summer (Brearley, 2005). However, the largest estuaries on the lower west coast remain permanently open and these include the Swan River, Peel-Harvey and Leschenault Estuaries, as well as Hardy Inlet (Hodgkin and Hesp, 1998; Brearley, 2005). During the summer and autumn, the lower reaches of these permanently-open estuaries essentially form an extension of the marine environment (Lenanton and Hodgkin, 1985; Fletcher and Head, 2006).

The coastline between Dunsborough (33°40´S, 114°59´E) and Geraldton (28°47´S, 114°37´E) is characterised by the presence of long sandy beaches, which are occasionally interspersed with small rocky cliffs and headlands. Large amounts of macrophytic detritus often accumulate in the nearshore waters of these sandy beaches and, together with the sheltered conditions in many areas, provide ideal nursery habitats for a number of fish species (Lenanton, 1982). The offshore marine environment along this stretch of coastline is characterised by typically coarse sand interspersed with low limestone reefs that are associated with past shorelines (Fletcher and Head, 2006). The

high-energy coast south of Cape Naturaliste is characterised by high granitic headlands that are interspersed with lunate bays (Commonwealth of Australia, 2006).

Although wave energy is moderate to high on the lower west coast (Lemm *et al*., 1999), a barrier of limestone reefs, shallow banks and islands along much of the coastline dissipates, on average, *ca* 60% of this energy (Masselink and Pattiaratchi, 2001). However, due to differences in the effects of wave shoaling, refraction, diffraction and breaking along this coast due to variations in the type and configuration of these offshore barriers, the extent to which the inshore waters are exposed to wave activity varies markedly (Valesini *et al*., 2003). Thus, while the wave heights at some nearshore sites are approximately half that of oceanic swell (Masselink and Pattiaratchi, 2001), they can be as small as 5% of those in offshore waters at other sites (Department of Environmental Protection, 1996). A number of large semi-sheltered lagoonal habitats are also present along this coastline, such as Cockburn Sound (32°12´S, 115°43´E), Jurien Bay (30°18´S, 115°01´E), Warnbro Sound (32°20´S, 115°43´E) and Geographe Bay (33°36´S, 115°15´E). However, such sheltered environments are rare southwards of Cape Naturaliste, with this region being exposed to heavy wave action driven by the West Wind Belt. During summer, the cool Capes Current flows nearshore and northward along the lower west coast (Pearce and Pattiaratchi, 1999; Gersbach *et al*., 1999), while the warm Leeuwin Current flows southward in the vicinity of the continental shelf in autumn to winter (Godfrey and Ridgway, 1985; Gersbach *et al*., 1999; Woo *et al*., 2006).

The marine flora and fauna on the lower west coast are predominantly of southern Australian affinity, but, due to the influence of the Leeuwin Current, which transports the propagules of many tropical species into temperate latitudes, there is also a strong Indo-West Pacific influence (Maxwell and Cresswell, 1981; Hutchins, 1991; Hutchins and Pearce, 1994; Commonwealth of Australia, 2006). The extended

distribution of tropical species is exemplified by the presence of hermatypic corals as far south as Geographe Bay and the regular occurrence of many species of tropical fish in the waters around Rottnest Island (32°01´S, 115°30´E) and along the south coast (see Section 2.1.3). The fauna also has a strong West Coast endemic element (Commonwealth of Australia, 2006). South of Cape Naturaliste, the species composition of communities is similar those of comparable habitats on the south coast. The larger estuaries support a depauperate fauna and flora, consisting of a few obligate estuarine species and a number of marine species that invade the estuaries opportunistically in summer (Potter and Hyndes, 1999).

Argyrosomus japonicus was mainly obtained from Geraldton and Perth on the lower west coast (Figs 2.1, 2.3a/b). At Geraldton, *A. japonicus* was obtained from nearshore waters and particularly near rock groynes in the vicinity of the wharf and from reef platforms situated along an exposed stretch of coast to the south of the Greenough River (Fig. 2.3a). In Perth, *A. japonicus* was obtained from Mosman Bay, *i.e.* in the lower reaches of the Swan River Estuary, from Cockburn Sound and from Perth's offshore waters, particularly near an artificial reef structure that is situated in *ca* 110 m of water south-west of Rottnest Island (Fig. 2.3b). Further samples of *A. japonicus* were obtained opportunistically from a number of surf beaches around Perth, as well as from the offshore waters of Dongara (29°17´S, 114°56´E), and the nearshore coastal waters of Bunbury (33°20´S, 115°38´E), Dunsborough (33°40´S, 114°59´E) and Augusta (34°19´S, 115°10´E) (Fig. 2.1).

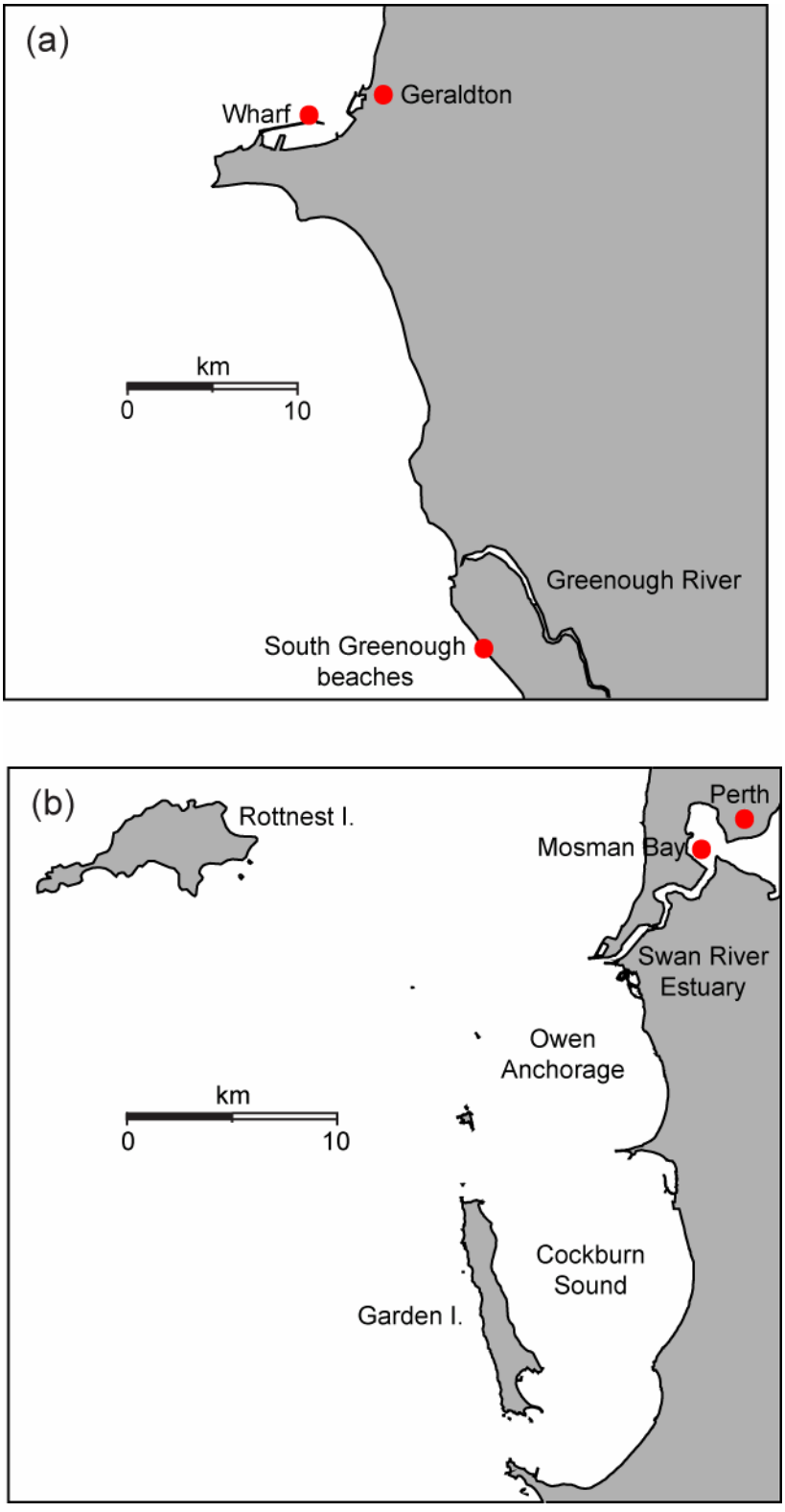


Figure 2.3. Map showing the main sampling locations for *Argyrosomus japonicus* on the lower west coast of Western Australia, which were located in (a) Geraldton and (b) Perth.

2.1.3 South coast

The south coast extends from Black Head in the west to Israelite Bay (33°35´S, 123°54´E) in the east and, under IMCRA, has been classified as a single bioregion, *i.e.* the Western South Coast (Commonwealth of Australia, 2006). The climate on the south coast ranges from temperate, with moderate to high rainfall in the west, to semi-arid in the east (Commonwealth of Australia, 2006). While estuaries are a prominent feature of this coastline, only the Walpole-Nornalup Estuary (34°59´S, 116°44´E) and Oyster Harbour (34°58´S, 117°57´E) remain permanently open, the remainder being either seasonally-open, normally-closed or permanently-closed (Hodgkin and Hesp, 1998). Furthermore, those of the more-arid east are fed by saline rivers (Hodgkin and Hesp, 1998).

Much of the south coast is characterised by prominent granite headlands, between which are located arcuate bays and white sandy beaches. The offshore marine environment includes granite outcrops, as well as occasional limestone reefs (Fletcher and Head, 2006). Coastal waters are clear and swept by the West Wind Drift and, since the continental shelf along this coastline is relatively narrow, it is exposed to very heavy swell (Commonwealth of Australia, 2006). However, the degree of exposure varies greatly, with a number of semi-sheltered and sheltered bays also being present, *e.g.* King George Sound in Albany, and thus coastal habitats are highly varied. The Leeuwin Current flows along the continental shelf in this region during the winter (Godfrey and Ridgway, 1985; Gersbach *et al*., 1999; Woo *et al*., 2006).

The coastal estuarine and marine flora and fauna are typically temperate, but with a significant local endemic element (Commonwealth of Australia, 2006). The Leeuwin Current introduces a few Indo-West Pacific stragglers (Maxwell and Cresswell, 1981; Hutchins, 1991; Hutchins and Pearce, 1994; Commonwealth of Australia, 2006). Extensive seagrass meadows are a feature of the sheltered bays and

inlets, while kelps dominate the rocky substrates in the sublittoral zone. Although these kelp habitats are diverse, they are dominated by *Ecklonia radiata* rather than the larger kelps expected in these latitudes (Fletcher and Head, 2006). There is a rich rocky shore intertidal fauna, but estuarine floras and faunas are generally depauperate due to the fact that the estuaries are mostly seasonally-open or normally-closed (*e.g.* Young and Potter, 2002; Brearley, 2005; Hoeksema, 2006; Hoeksema *et al*., 2006). Nevertheless, some of the estuaries remain very productive, with Oyster Harbour having the highest diversity of invertebrate fauna and Wilson Inlet supporting the largest commercial and recreational estuarine fisheries on the south coast (Brearley, 2005; Commonwealth of Australia, 2006).

Argyrosomus japonicus was collected from Oyster Harbour and the lower reaches of the Kalgan River in Albany (Fig. 2.4). While "physically" an estuary, Oyster Harbour is hydrologically and ecologically a marine embayment similar to the nearby Princess Royal Harbour (Hodgkin and Hesp, 1998; Brearley, 2005). The flow from its two main tributaries, *i.e.* the Kalgan and King Rivers, is small (10^6 m^3) and since any flood water is quickly lost to sea as surface flow, its lagoonal waters are rarely diluted by fresh water (D'Adamo *et al*., 1992). Unlike most estuaries on the south coast, tidal flow is not reduced by the presence of a bar. While the water level generally only varies between 0.3 and 1.2 m daily, the narrow entrance channel of Oyster Harbour creates a fast tidal flow that has scoured this region of the estuary to a depth of 10 m (Hodgkin and Hesp, 1998; Brearley, 2005). While the Kalgan River is 2-3 m deep along much of its length, with some depressions on the river bends being as deep as 4 m, the main channel gradually shallows in the lower reaches to a depth of only 1 metre (Brearley, 2005). Approximately 70% of the catchment for Oyster Harbour has been extensively cleared for agriculture, and high nutrient levels in the run-off has lead to the sporadic eutrophication of this system (Hodgkin and Clark, 1990; Fletcher and Head, 2006).

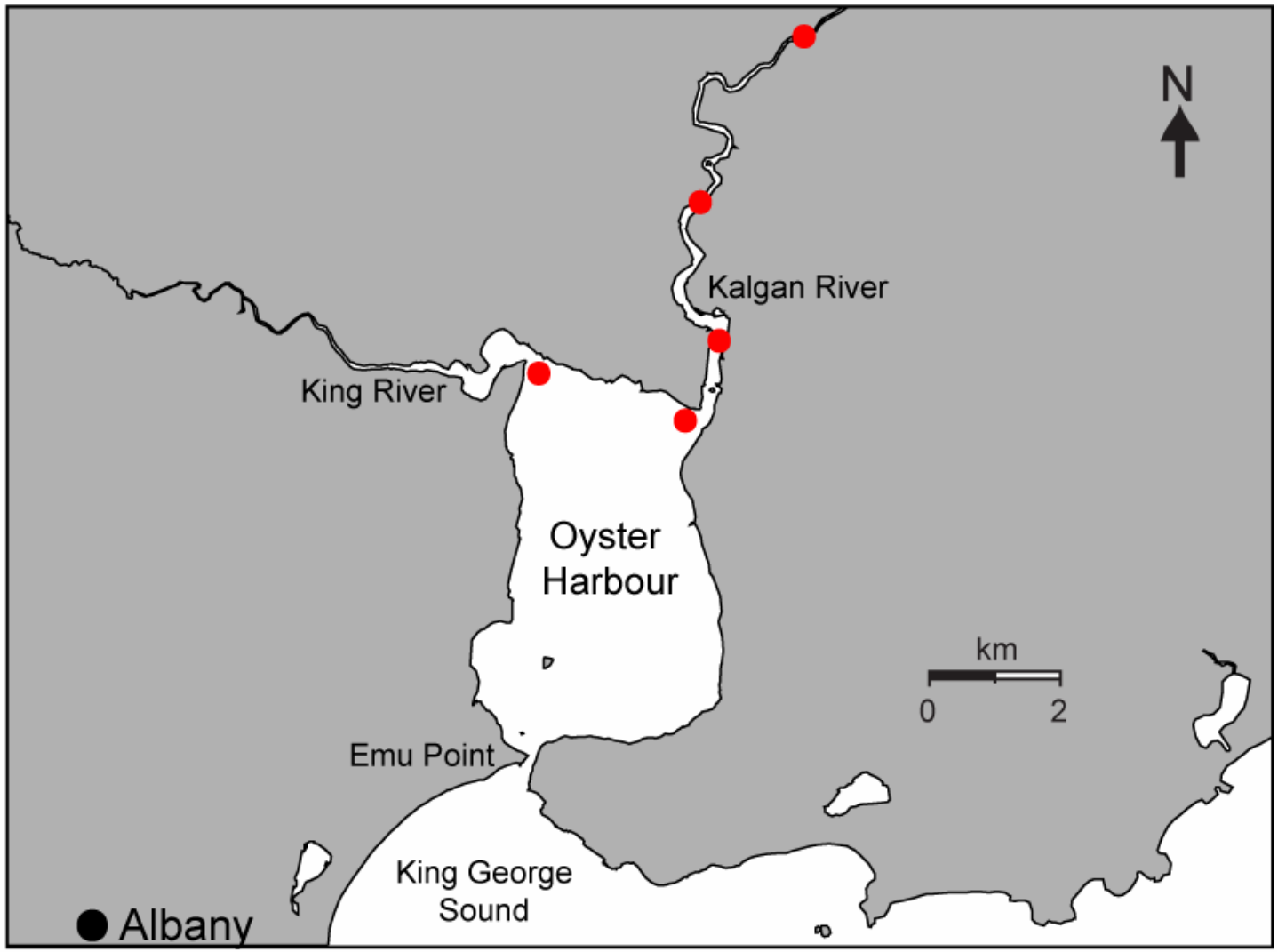


Figure 2.4. Map showing the main sampling locations (solid red circles) for *Argyrosomus japonicus* on the south coast of Western Australia.

2.2 Sampling regime

The majority of *Argyrosomus japonicus* caught on the upper and lower west coasts were obtained by rod and line angling, while those on the south coast were all collected using composite sunken gill nets (Table 2.1). The possibility of introducing a size-selective bias by hook size during rod and line angling was minimised by using at least two different types of rigs on the majority of occasions, with each of these having very different hook sizes. The first was a "paternoster rig" set up with a sinker on the bottom (weight dependent on conditions), above which were two dropper loops that each terminated with a size 6 long shank hook, *i.e.* similar to the "whiting boat rig" outlined in Cusack and Roennfeldt (2002). The second rig was set up with a sinker running freely on the main line (type and weight again dependent on conditions) down to a swivel and *ca* 60 cm of trace line with two size 6/0 to 9/0 hooks that were snelled *ca* 10 cm apart, *i.e.* similar to the "South Australian mulloway rig" outlined in Cusack and Roennfeldt (2002). Gill nets comprised six panels, each with a length of 20 m and a height of 2 m and containing a different stretched mesh size, *i.e.* 51, 63, 76, 89 or 102 mm. These nets were laid parallel to the shore at dusk and were set for 1h.

On the upper west coast, the Western Australian Department of Fisheries provided data for *A. japonicus* that were caught by seine netting the nearshore waters of Miaboolya Beach in Carnarvon. The 40.5 m seine net contained two 20 m long wings, consisting of 25 mm mesh and a 1.5 m wide central bunt made of 9 mm mesh. This net, which was walked out in a semi-circle outwards from the shore and then hauled on to the beach, fished to a maximum depth of 2 m and swept an area of 274 m^2. On the lower west coast, despite extensive gill netting in the Swan River and regular surveys of prawn trawl by-catch in Mandurah coastal waters, only eight individuals were obtained by these methods (Table 2.1). Further samples were obtained opportunistically by spear fishing and by collecting dead individuals from the banks of the Swan River (Table 2.1).

As revealed by their identifying Australian National Sportfishing Association (ANSA) tags, several of these dead fish had been caught and released by recreational anglers the previous night. Further samples of *A. japonicus* were obtained from recreational anglers in Kalbarri and Perth and, subsequent to filleting, from wholesale fish markets in Geraldton and Perth. While the method of capture was determined for all commercial samples of *A. japonicus* obtained (with these data also included in Table 2.1), the majority of these samples were caught by wetline fishers that mainly targeted Pink Snapper *Pagrus auratus* in the Carnarvon Basin.

Table 2.1. Summary of the sample sizes and percentage contributions of *Argyrosomus japonicus* collected by each method of capture in each sampling region

Method	Upper west coast		Lower west coast		South coast	
	n	**%**	***n***	**%**	***n***	**%**
Line	687	92.6	309	95.1		
Gill net			3	0.9	272	100
Seine net	54	7.3				
Trawl			5	1.5		
Spear	1	0.1	3	0.9		
Dead			5	1.5		
Total	**742**		**325**		**272**	

2.3 General laboratory procedures

The total length and wet weight of each *A. japonicus* obtained during sampling was measured to the nearest 1 mm and 1 g, respectively. Whenever possible, each fish collected from the fish market was weighed whole prior to filleting and its total length and weight recorded to the nearest 1 mm and 10 g, respectively. The weights of all other *A. japonicus* that could not be obtained prior to filleting were estimated from the regression equation that relates the wet weight to total length for this species (Chapter

3.3.5). More specific methods are detailed in the Materials and Methods sections of each of the data Chapters 3-5.

3.0 Length and age compositions and growth

3.1 Introduction

3.1.1 Ageing of teleost fishes

Estimating the age of individual fish within a population provides the basis for determining the age composition, growth rate and mortality of that population, which represent three of the life history characteristics that most influence the productivity of fish stocks (Campana and Thorrold, 2001). The fact that age-related population demographics can also be used in models for assessing the impacts of commercial and recreational fishing (Beverton and Holt, 1957; Millar and Meyer, 2000), accounts for the determination of fish age being one of the most routine procedures in fisheries science. While determining the age structure of fish populations has been sought through the implementation of a variety of different methods (see Campana, 2001), the enumeration of annuli in hard structures, and particularly otoliths, has been favoured in recent times. The preference for otoliths over other hard structures is due to their unparalleled chronological properties, *i.e.* the potential to allow for the determination of daily as well as annual age, and their unique mode of calcification that renders them impervious to any form of metabolic reworking (Payan *et al.*, 1997; Campana, 1999; Campana and Thorrold, 2001).

The estimation of fish age based on the number of growth zones in otoliths incorporates two major sources of error, namely a process error associated with the chronological properties of the structure under examination and an interpretation error due to the subjectivity required of all age estimations (Campana, 2001). Process error can arise due to the fact that not all calcified structures or, indeed, all axes on a single structure (Beamish, 1979), form a complete growth sequence throughout the entire lifetime of a fish (Campana, 2001). Interpretation error can arise due to variation in the preparation of the selected calcified structure and the interpretation of its periodic features, which can vary markedly among readers and/or laboratories (Boehlert, 1985;

Campana and Moksness, 1991). The prevalence and impact of such process and interpretation errors on age determinations and their subsequent effect on the accuracy of studies of fish population dynamics have been reviewed by Campana (2001). They usually result in underestimations of age in long-lived species, which can lead to overly optimistic estimates of growth and mortality and thus the implementation of unsustainable harvest strategies. This pattern of mismanagement has been particularly common amongst deep-sea fisheries, such as those of the Orange Roughy *Hoplostethus atlanticus* off New Zealand (Smith *et al*., 1995) and Redfish *Sebastes* spp. off the eastern and western coasts of Canada (Chilton and Beamish, 1982; Campana *et al*., 1990). However, given the relative longevity of certain members of a number of families of inshore fishes, such as the Labridae (*e.g.* Gillanders, 1995; Sadovy *et al*., 2003; Choat *et al*., 2006), Lutjanidae (*e.g.* Wilson and Nieland, 2001) and Sciaenidae (*e.g.* Griffiths and Hecht, 1995a), mismanagement due to ageing error is certainly not exclusive to waters beyond the continental shelf. Since the use of inaccurate ages can lead to substantial errors in fishery management, ensuring ageing accuracy and quantifying ageing precision should be considered essential components of any age-related study (Campana, 2001).

The most common form of ensuring ageing accuracy is the implementation of an age validation procedure, which can be classified as either validating absolute age or the periodicity of growth increment formation or corroborating an existing set of age estimates (Beamish and McFarlane, 1983; Campana, 2001). While there are a variety of age validation techniques suitable for estimating annual age (Blacker, 1974; Bagenal and Tesch, 1978; Casselman, 1983, 1987; Cailliet *et al*., 1986; Beamish and McFarlane, 1987; Campana, 1999, 2001), the use of marginal increment analyses to validate the periodicity of annual growth increment formation is one of the most common approaches. The marginal increment, *i.e.* the distance between the outer edge of the

outermost opaque zone and the periphery of the otolith, is measured and expressed as a proportion of the distance between the primordium and the outer edge of the single opaque zone, when only one such zone is present, or as the distance between the outer edges of the two outermost opaque zones, when more than one opaque zone is present. If an opaque zone is formed annually, the average state of completion of the outermost increment for each month or season should display a cycle with a frequency of one year (Campana, 2001). The interpretation of the marginal growth increment should also extend to defining the type of zone on the growing edge, *i.e.* opaque or translucent. This can influence the accuracy of ageing at the annual level, since an annulus on the margin of a structure collected just after the birth date (usually inferred from the time of peak spawning) can be allocated a different age to the same structure collected just before that birth date. Thus, the age assigned to a fish is a function of not only the number of annuli, but also of "edge type" in relation to the date of collection and the assigned birth date. Although the incorporation of an age validation procedure equips a study to deal with process error, interpretation error is generally not taken into account (Campana, 2001). Campana (2001) has suggested that this may be overcome by laboratories archiving reference materials, *e.g.* photo libraries of sectioned otoliths, which could be shared amongst fishery scientists on the World Wide Web and thus facilitate discussion of any differences in interpretation.

Ageing precision, *i.e.* the reproducibility of repeated measurements on a given structure (Campana, 2001), has most commonly been quantified by reporting the percent agreement between two independent readers. While easy to interpret, this method is not appropriate for comparing different stocks or species as it does not take into account the age composition of each sample (Beamish and Fournier, 1981; Chang, 1982; Kimura and Lyons, 1991; Lai *et al*., 1996; Campana, 2001). For example, Beamish and Fournier (1981) noted that 95% agreement to within one year between two

age readers of Pacific cod *Gadus macrocephalus* constituted poor precision, particularly given the few year classes in that fishery, while 95% agreement to within five years would constitute good precision for spiny dogfish *Squalus acanthias* due to its 60 year longevity. Two widely used and statistically sound measures of ageing precision that do take into account the age composition of the sample are the average percent error (APE; Beamish and Fournier, 1981) and the coefficient of variation (CV; Chang, 1982). A review of the frequency of use of each of these methods, together with a summary of the published values of CV, has been provided by Campana (2001). Since ageing precision is highly influenced by the nature of the calcified structure being examined, and even the species from which that structure came, and thus not just the age reader, Campana (2001) stated that there is no *a priori* value that can be designated as a target level for all ageing studies. However, for many fishes of moderate longevity and reading complexity, that author suggests that a CV of 5% serves as an adequate reference point.

An accurate determination of the age of individual fish within a population provides information that can be used to estimate longevity, age at first maturity and the age at first recruitment into the fishery. Furthermore, reliable age data can also be incorporated into one of a multitude of mathematical equations that are applied to model the average growth of fish within a given population. While there are a number of models that have been fitted to length-at-age data for teleost fish (*e.g.* von Bertalanffy, 1957; Schnute, 1981; West *et al*., 2001; Lester *et al*., 2004), the model proposed by von Bertalanffy (1957) remains the most common. Regardless of the model selected, the fitting of growth curves facilitates comparisons of the growth of fish, such as between populations that are distributed over wide latitudinal ranges and/or which occur in different environments. In this context, a number of fish species have been shown to grow faster at higher than lower latitudes (*e.g*. Conover *et al*., 1997; Jonassen *et al*., 2000; McBride *et al*., 2002).

3.1.2 Results of previous studies on *Argyrosomus japonicus*

Although *A. japonicus* constitutes an important component of commercial and recreational catches throughout its entire Indo-Pacific distribution (Griffiths and Heemstra, 1995), age-related information is not available throughout this range. In fact, there are no age-related studies published for wild populations of *A. japonicus* north of the equator. However, there have been studies on various aspects of the biology of captive-reared *A. japonicus* in Taiwan, where this sciaenid is cultured in saltwater net cages (Ueng *et al*., 2007). In this environment, *A. japonicus* is reported to attain lengths of 700 to 800 mm in five to six years (Lin *et al*., 1998). However, since one of the main aims of aquaculture is to optimise fish growth, the extent to which the growth rates recorded in this study are considered to reflect accurately those of wild populations of *A. japonicus* in Taiwan must be treated with caution.

In the Southern Hemisphere, studies of wild populations of *A. japonicus* have been carried out in both South Africa and Australia. In South Africa, there are peer-reviewed and published investigations of the age structure and growth of *A. japonicus*, which were based on reliable estimates of age derived from sectioned otoliths (Wallace and Schleyer, 1979; Griffiths & Hecht, 1995a). However, the study of Wallace and Schleyer (1979) was based predominantly on relatively young fish, *i.e.* < 12 years of age and with all but seven of the 148 fish examined being younger than 7 years. Griffiths and Hecht (1995a) provide the most detailed and reliable age-related study of *A. japonicus* in South Africa, which involved the examination of a large number of samples, with these varying in length from 35 to 1750 mm, and included a validation procedure to confirm the annual periodicity of growth zone formation. Excluding one female of 42 years and one male of 30 years, it was determined that the age distributions were similar for both sexes throughout that region (Griffiths and Hecht, 1995a). These authors found that a modified four-parameter von Bertalanffy growth equation, *i.e.*

$L_t = L_\infty \left(1 - \exp^{-k(t-t_0)}\right)^p$, provided a statistically better fit to the lengths at age of South African *A. japonicus* than the traditional three-parameter von Bertalanffy equation. The modified four-parameter model demonstrated that the growth of both sexes was rapid until the end of their eighth year of life, when the females and males had attained, on average, total lengths of 1131 and 1171 mm, respectively. Growth in both sexes slowed markedly in all subsequent years, but more so for males than for females, *i.e.* values of L_∞ were 1372 mm and 1473 mm for males and females, respectively (Griffiths and Hecht, 1995a).

While a number of age-related studies have been carried out on *A. japonicus* in Australian waters, most of these have not included a validation procedure and rarely have they described the growth of *A. japonicus* throughout its entire life cycle. For example, Gray and McDonall (1993) described the growth of juvenile *A. japonicus* using individuals caught as by-catch of prawn trawling in the Hawkesbury River, while Holt (1978) examined mainly adult fish in the Swan River Estuary. Hall (1986) included fish of a wide size range from South Australian waters, but his ages were based on counts of the circuli in scales that were not validated as being formed annually. Furthermore, given the propensity for scales to lead to underestimates of age (Simkiss, 1974; Booth *et al*., 1995; Campana and Thorrold, 2001), particularly for relatively long-lived species (*e.g.* Barnes and Power, 1984; Howland *et al*., 2004), these results should be considered with caution. More recently, Silberschneider and Gray (2005) described the growth of *A. japonicus* in New South Wales waters using a relatively large sample, which included individuals of 50 to 1690 mm in total length, and estimates of age derived from the number of opaque zones in sectioned otoliths. Since this study also included marginal increment analysis to validate the annual periodicity of opaque zone formation in otoliths, these results are the most reliable to date for Australian *A. japonicus*. However, since the sex of many fish obtained from commercial sources

could not be determined during that study, the length or age distributions of each sex were not given and only a single growth curve was provided. Nevertheless, fish of 0-24 years were examined and, as for South African *A. japonicus*, growth was particularly fast during their early life. For example, fish had attained, on average, lengths of 347, 520 and 780 mm by the end of their first, second and fourth years of life. Growth slowed in subsequent years, with the value of L_{∞} being 1317 mm.

3.1.3 Aims

The aims of this component of the thesis, which focuses on *A. japonicus* from the upper and lower west coasts of Western Australia and on an assemblage on the south coast of this state, were as follows. 1) Validate that opaque zones are formed annually in the otoliths of *A. japonicus* in Western Australian waters and their numbers can thus be used to age the individuals of this species. 2) Quantify the precision of opaque zone counts using the coefficient of variation. 3) Use reliable estimates of age to describe and compare the patterns of growth of female and male *A. japonicus* on the upper and lower west coasts of Western Australia. It is hypothesised that the growth of *A. japonicus* in comparable marine waters is greater at higher than lower latitudes, *i.e.* on the lower west than upper west coast. 4) Compare the growth of *A. japonicus* in an estuary (Oyster Harbour) on the south coast with those in coastal waters on the upper and lower west coasts. Note that the individuals caught in Oyster Harbour comprised smaller and younger fish and that such fish were found only in coastal waters on the upper and lower west coasts.

3.2 Materials and methods

3.2.1 Removal and preparation of otoliths

The sagittal otoliths of each *Argyrosomus japonicus* were excised by removing the gill rakers and cutting away a portion of bone on the left side of the prootic/exoccipital region. The otoliths were then washed, dried and stored in labelled paper envelopes. The otoliths of *A. japonicus* were sectioned because they are particularly thick and their opaque zones were not clearly visible when the otoliths were viewed whole (Fig. 3.1). The left otolith of each fish (unless damaged, in which case the right otolith was used) was embedded in clear epoxy resin and, using a low-speed diamond saw, cut through its central region into 2-3 longitudinal sections to ensure that the primordium was included. These sections, which ranged in thickness from 450 to 750 µm, were mounted on glass slides and viewed under reflected light against a black background using a Leica MZ7.5 dissecting microscope.

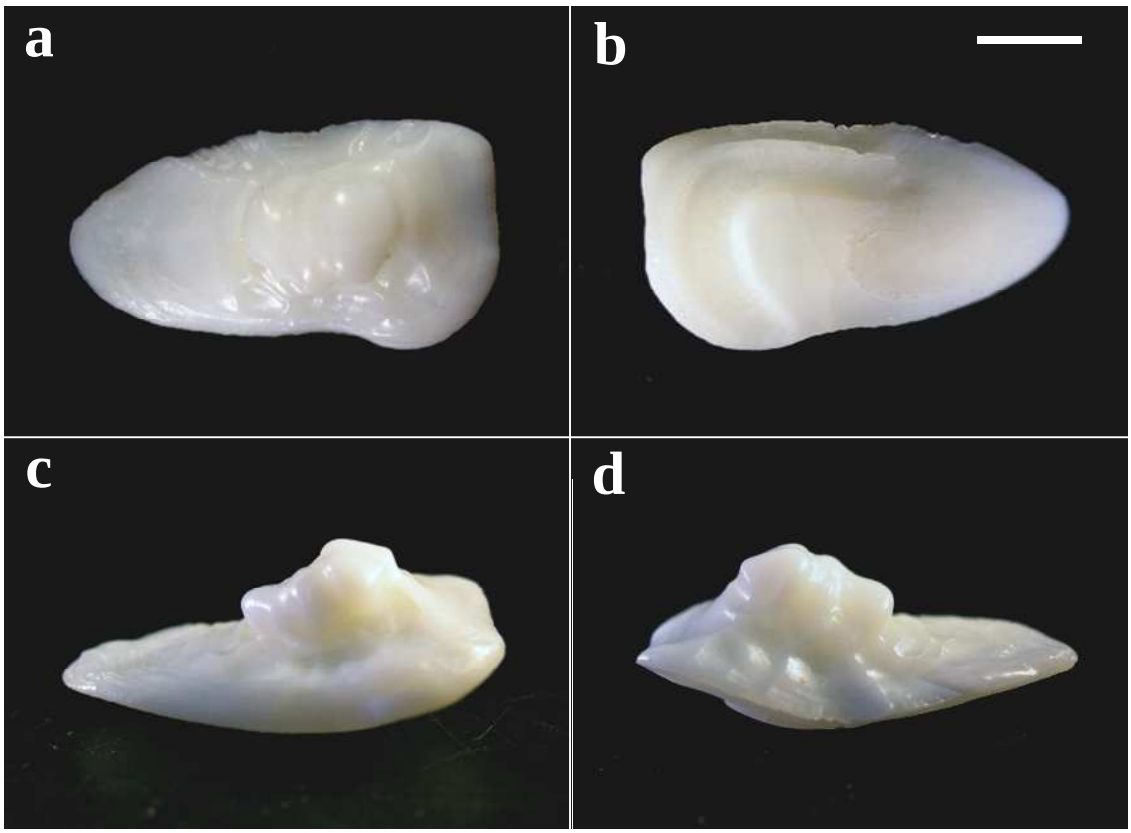


Figure 3.1. A typical sagittal otolith of *Argyrosomus japonicus* (1143 mm total length), showing the (a) lateral, (b) medial, (c) dorsal and (d) ventral surfaces. Scale bar = 5 mm.

3.2.2 Marginal increment analysis

Validation that a single growth zone is formed each year in the otoliths of *A. japonicus* was undertaken by analysing the trends exhibited throughout the year by the marginal increment, *i.e.* the distance between the outer edge of the outermost opaque zone and the periphery of the otolith. For this purpose, the marginal increment was expressed either as a proportion of the distance between the primordium and the outer edge of the opaque zone, when only one opaque zone was present (Fig. 3.2a), or as a proportion of the distance between the outer edges of the two outermost opaque zones, when two or more opaque zones were present (Fig. 3.2b). The above measurements were made along the same axis, perpendicular to the opaque zone(s) and in the region beneath the cauda where the alternating opaque and translucent zones were particularly well defined (Fig. 3.2a, b). All measurements were made without knowledge of the date of capture of the fish from which that otolith had been removed and were recorded to the nearest 0.01 mm using the computer imaging software Leica IM1000 (Leica Microsystems Ltd., 2001) and images obtained via a Leica DC300 digital camera that was attached to the Leica MZ7.5 dissecting microscope. The marginal increments in otoliths with the same number of opaque zones were then pooled and the mean and standard error calculated for each calendar month to ascertain the within-year trend. Since the trends exhibited by the mean monthly marginal increment for *A. japonicus* on the upper west, lower west and south coasts showed no indication of differences, the data for all regions was combined.

3.2.3 Ageing procedure and ensuring precision

The opaque zones in otoliths were counted in the region beneath the cauda, where the alternating translucent and opaque zones were particularly well defined (Fig. 3.2a, b).

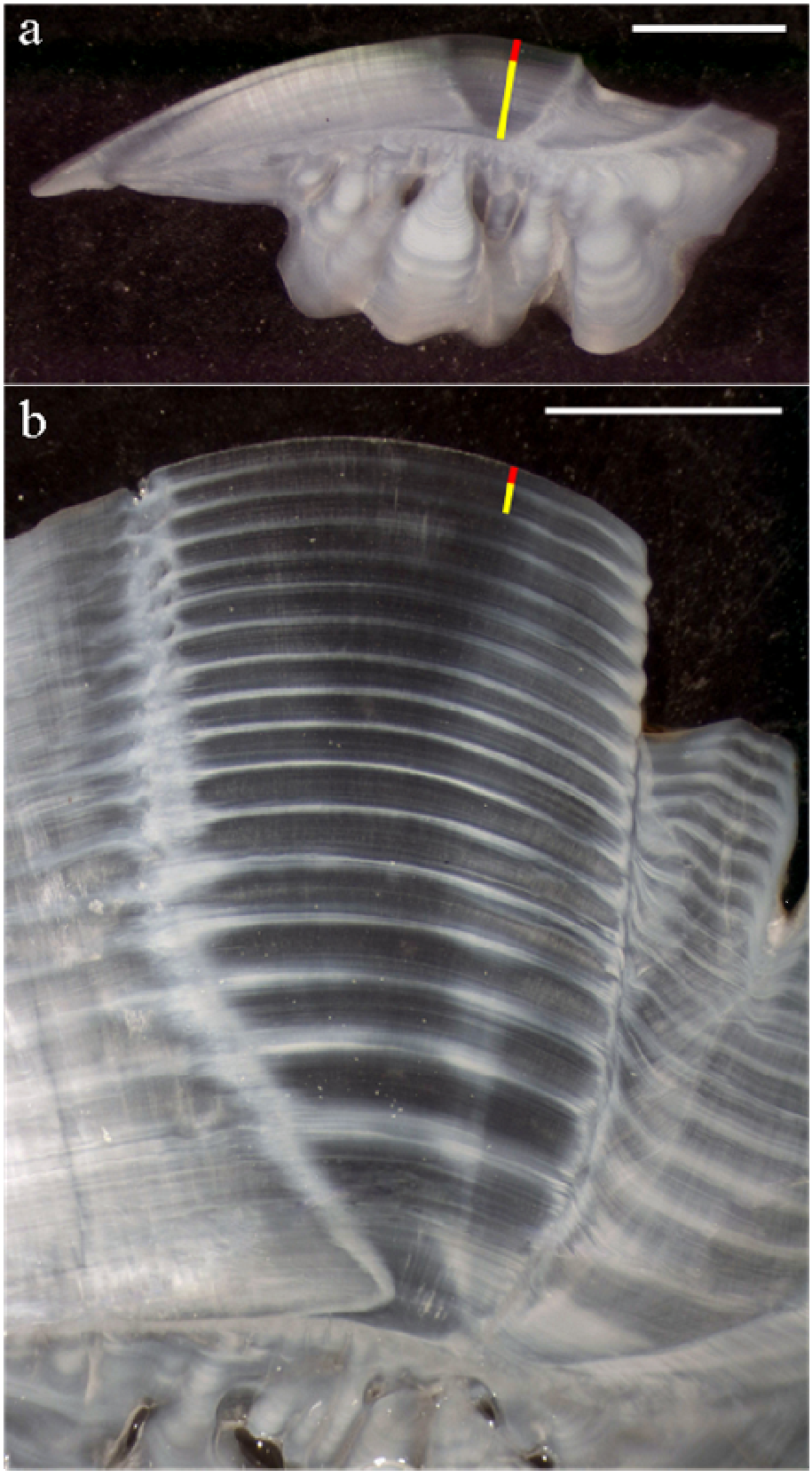


Figure 3.2. Longitudinal sections through the primordium of sagittal otoliths of *Argyrosomus japonicus* containing (a) 1 opaque zone and (b) 17 opaque zones, which were photographed under reflected light against a black background. Yellow and red lines indicate the locations of measurements taken for marginal increment analysis. Scale bars = 2 mm.

The opaque zones in each otolith were counted three times, at least one week apart, and without knowledge of either the length and date of capture of the fish from which that otolith had come or the results of any prior counts. In the few cases when the three counts were not the same, two of those counts were the same and these were adopted as the count. The precision of opaque zone counts was quantified using the mean coefficient of variation (CV; Chang, 1982). Since the CV value was low, *i.e.* 0.72%, and well below the reference point of 5% suggested by Campana (2001), counts were of a high level of precision.

Ages were assigned to each *A. japonicus* on the basis of the number of opaque zones (annuli) in their otoliths, while taking into account the time of year that these opaque zones become delineated from the periphery of otoliths, the date of collection and the assigned birth date of the fish. Furthermore, if the date of capture was close to the time of year when opaque zones became delineated from the edge of otoliths, consideration was also given to whether the otolith possessed an opaque or translucent zone at its periphery. The birth dates assigned to *A. japonicus* on each of the upper west, lower west and south coasts corresponded to the mid-point of the period when, on the basis of gonadosomatic indices and/or the trends shown by gonadal and oocyte development, this species spawns in each of these regions. The assigned birth dates for *A. japonicus* were 1 July on the upper west coast, 1 December on the lower west coast and 1 November on the south coast (see Chapter 4).

3.2.4 Analysis of growth

The von Bertalanffy growth model was fitted to the lengths at age of the females and males of *A. japonicus* caught in each of the sampled regions, *i.e.* upper west coast, lower west coast and south coast, using non-linear regression in the Statistical Package for the Social Sciences software (SPSS 15.0 for Windows; SPSS Inc., 2006). The lengths at age

of small juvenile fish whose sex could not be determined were randomly but equally allocated to the female and male data sets used for calculating the growth curves. The von Bertalanffy growth equation is $L_t = L_\infty\left(1-\exp^{-k(t-t_0)}\right)$, where L_t is the estimated total length at age t (years), L_∞ is the asymptotic length predicted by the equation, k is the growth coefficient (year^{-1}), *i.e.* a parameter determining the rate at which L_t approaches L_∞, and t_0 is the hypothetical age (years) at which fish would have zero length, if their growth had followed that predicted by the equation. The von Bertalanffy growth equations and associated parameters for the females and males of *A. japonicus* in each region were compared using a likelihood-ratio test. The hypothesis that a common growth curve could be used for the two sexes was rejected at the $\alpha = 0.05$ level of significance if the test statistic, calculated as twice the difference between the log-likelihood obtained by fitting a common growth curve for both sexes and by fitting separate growth curves for each sex, exceeded $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters in the two approaches (*e.g.* Cerrato, 1990). The log-likelihood was calculated (ignoring constants) as $-(n/2)\times\log_e(ss/n)$, where n is the total number of female and male fish and *ss* is the sum of the squared deviations between the observed and predicted lengths at age of the combined set of data for both female and male fish. The residuals from each of the analyses were calculated, standardized by dividing by their standard deviation, and plotted against age to ascertain whether the resulting growth curves deviated systematically from the observed lengths at age. The same likelihood-ratio test was then used to test whether the growth curves differed between regions.

The growth of South African *A. japonicus* has been described by Griffiths and Hecht (1995a) by introducing an additional parameter, *p*, into the von Bertalanffy growth equation as follows; $L_t = L_\infty\left(1-\exp^{-k(t-t_0)}\right)^p$. Since, during that study, the

modified 4-parameter model provided a statistically better fit than the traditional 3-parameter model, it was also fitted to each of the data sets in the present study. The standardized residuals for the estimated lengths of *A. japonicus* in each of the three regions, derived from the use of the 4-parameter von Bertalanffy growth equation, were plotted and compared with those derived using the 3-parameter von Bertalanffy equation. The likelihood-ratio test, as described earlier, was used to determine whether the growth curve fitted using the 4-parameter model for females and males on the upper west, lower west and south coasts were significantly different. The same likelihood-ratio test was then used to test whether the growth curves differed between regions.

The likelihood-ratio test was used to determine whether the 4-parameter model improved the predicted lengths at age of fish in each of these regions from those that were produced using the traditional, unadjusted von Bertalanffy model. Whether or not the 4-parameter model provided better resolution than the 3-parameter model determined which of the models was used to provide data to base subsequent comparisons between the growth of *A. japonicus* in different regions.

3.2.5 Relationship of total length to weight

The relationships between total length (*TL* in mm) and weight (*W* in g) of females and males were determined by linear regression of the logarithmically-transformed data, *i.e.* employing natural logarithms. The length-weight relationships for females and males of *A. japonicus* were then compared using analysis of covariance (ANCOVA) and employing $\log_e W$ as the dependent variable, sex as the fixed factor and $\log_e TL$ as the covariate. ANCOVA was also employed to test for any regional differences in the relationship between $\log_e TL$ and $\log_e W$. Note that when $\log_e W$ was back-transformed to determine the weight of a fish, the correction factor, exp(mean of squared residuals/2),

was employed to take into account any bias introduced with the logarithmic-transformation (Beauchamp and Olson, 1973).

3.3 Results

3.3.1 Validation of annuli

The mean monthly marginal increment on sectioned otoliths of *A. japonicus* with 2-4 opaque zones remained at 0.5-0.6 from July to November and then declined precipitously to *ca* 0.15 in December and January, after which it increased progressively to *ca* 0.5 in April and remained at about that level in the immediately ensuing months (Fig. 3.3). Similar trends were exhibited by the mean monthly marginal increment on otoliths with 5-7 and ≥ 8 opaque zones (Fig. 3.3). Although none of the fish caught in October and January contained otoliths with 1 opaque zone and the numbers of fish with otoliths having only one opaque zone were low in several other calendar months, the mean monthly marginal increment on otoliths with one such zone could still clearly be seen to follow a similar trend to that exhibited by otoliths with two or more opaque zones (Fig. 3.3). The presence, during the year, of a single marked decline and subsequent rise in the mean monthly marginal increments demonstrate that, irrespective of the number of opaque zones, a single opaque zone is typically formed annually in the otoliths of *A. japonicus*. Furthermore, the trends exhibited by the mean monthly marginal increments demonstrate that each new opaque zone becomes delineated by the formation of a new translucent zone in November/December, *i.e.* late spring/early summer.

3.3.2 Length and age compositions

The length and age distributions of females were similar to those of males in each of the three sampling regions (Fig. 3.4). On the upper west coast, *A. japonicus* ranged from 53 to 1293 mm in length and from 0 to 25 years in age, with the majority of fish belonging to the 0+ to 7+ age classes and the age distribution becoming discontinuous above 15

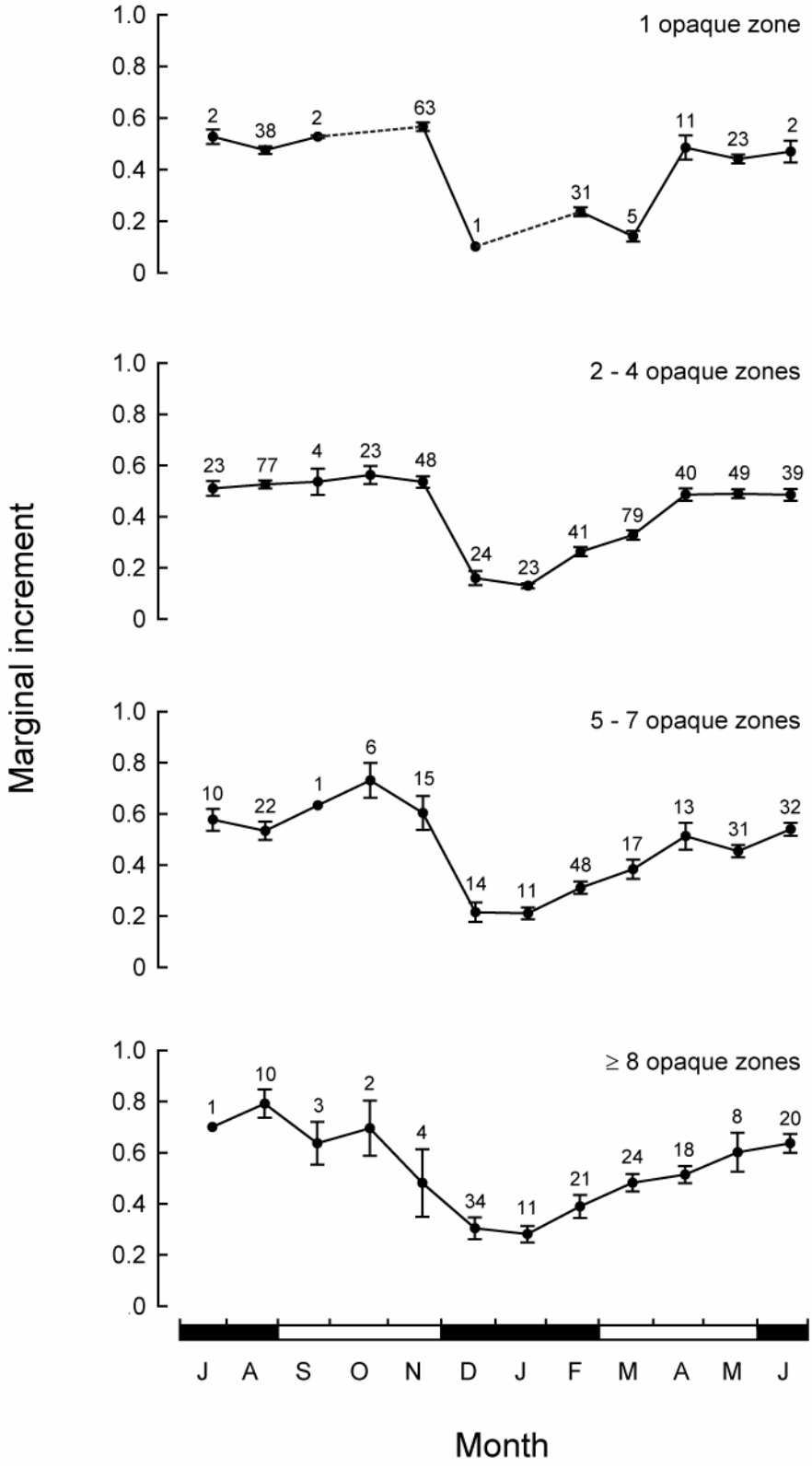


Figure 3.3. Mean monthly marginal increments ± 1 standard error for sectioned sagittal otoliths of *Argyrosomus japonicus*. Sample size is given for each month. On the x-axis, closed rectangles represent the winter and summer months and open rectangles the spring and autumn months.

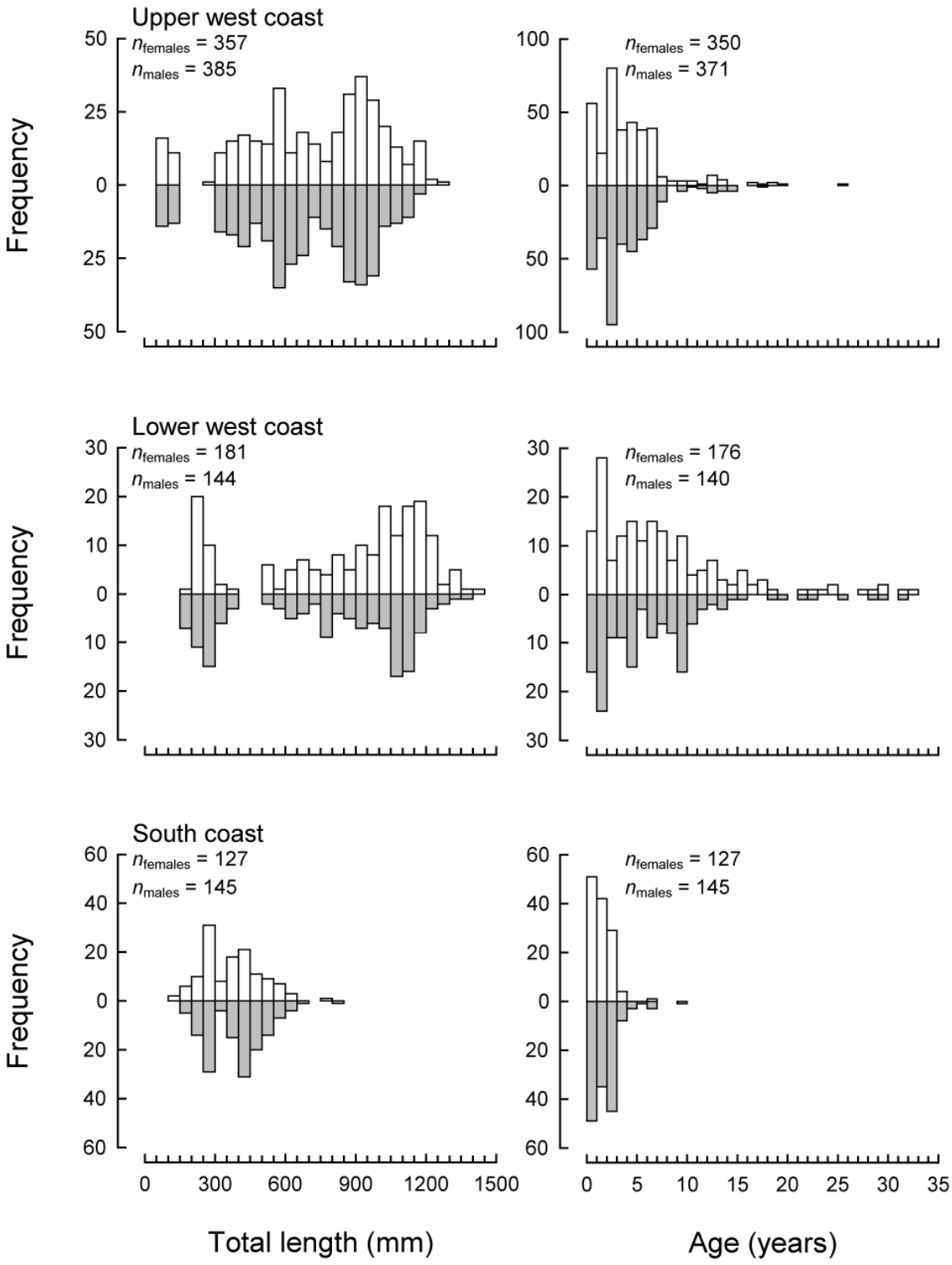


Figure 3.4. Total length and age-frequency distributions for females (white histograms, above x-axis) and males (grey histograms, below x-axis) of *Argyrosomus japonicus* caught on the upper west, lower west and south coasts of Western Australia between 2001 and 2006.

years (Fig. 3.4). On the lower west coast, *A. japonicus* ranged from 150 to 1437 mm in length and from 0 to 32 years in age, with the majority of individuals belonging to the 0+ to 16+ age classes and relatively few individuals exceeding 17 years in age (Fig. 3.4). The *A. japonicus* collected from the south coast were far more restricted in size and age, *i.e.* ranged from 127 to only 813 mm in length and from 0 to only 10 years in age, with the majority of fish lying between 200 and 600 mm in length and belonging to the 0+ to 4+ age classes (Fig. 3.4).

3.3.3 Fitting of the growth models

The likelihood-ratio test demonstrated that, irrespective of whether the traditional 3-parameter or adjusted 4-parameter von Bertalanffy models were employed, the growth curves of the females and males of *A. japonicus* on each of the upper west, lower west and south coasts were significantly different ($p < 0.05$). Thus, for subsequent comparisons between these two growth models, the lengths at age of females and males were kept separate. Comparisons between the distributions of the standardized residuals derived from fitting the 3-parameter and 4-parameter growth curves indicated that the latter of these provided an equivalent or better fit to the lengths at age of the females and males of *A. japonicus* in each region. Since the likelihood-ratio test confirmed that the adjusted 4-parameter von Bertalanffy model provided an equivalent or significantly better description when fitted to each of the data sets (Table 3.1), this model was used for all subsequent analyses and comparisons of growth. However, as the traditional 3-parameter von Bertalanffy model also provided a good fit to the lengths at age of the females and males in each region and has been applied much more frequently for other species, parameter estimates for this model are provided along with those for the 4-parameter model (see Table 3.2).

Table 3.1. The log-likelihoods determined for the traditional 3-parameter and modified 4-parameter von Bertalanffy growth models and the results of the likelihood-ratio tests comparing the two models for each data set. S = significant (**$p < 0.01$; ***$p < 0.001$), NS = not significant ($p > 0.05$).

Data set		Log-likelihoods		L-ratio test
		3-parameter	4-parameter	
Upper west coast	Females	-1580.93	-1573.56	S**
	Males	-1626.34	-1615.36	S***
Lower west coast	Females	-746.62	-745.84	NS
	Males	-611.84	-601.40	S***
South coast	Females	-442.43	-442.33	NS
	Males	-505.93	-505.00	NS

3.3.4 Comparisons of growth

As the likelihood-ratio test demonstrated that the von Bertalanffy growth equations fitted to the lengths at age of females and males of *A. japonicus* on the upper west coast did not differ significantly from those of the corresponding sexes on the lower west coast ($p > 0.05$), the lengths at age of the females and of the males in these two regions were pooled. While it should be kept in mind that the south coast sample of *A. japonicus* was collected from a single estuary that contained individuals with a restricted range of lengths and ages, the likelihood-ratio test further demonstrated that the von Bertalanffy growth equations fitted to the lengths at age of females and males of *A. japonicus* in this region were highly significantly different from those of the corresponding sexes on the combined west coast ($p < 0.001$). Note also that the growth of *A. japonicus* on the west and south coasts will be compared later in this chapter following truncation of the length-at-age data sets to four years of age, to accommodate the fact that most individuals on the south coast were below this age.

The 3-parameter and modified 4-parameter von Bertalanffy growth equations provided good fits to the lengths at age of the females and males of *A. japonicus* on the west coast, as is demonstrated by the high coefficients of determination (r^2) of 0.930 and 0.928, respectively, and values for t_0 that are close to zero (Table 3.2). The lengths at each successive age for females and males of *A. japonicus* on the west coast, as derived from the von Bertalanffy growth equations, were very similar for the first 5 years, after which age growth slowed markedly and, to a slightly greater extent, in males than females (Fig. 3.5). The divergence in growth at 5 years of age of the females and males on the west coast accounts for the significant differences in L_∞ ($p < 0.05$), which is further reflected in the greater asymptotic length of the females than males in this region, *i.e.* 1228 mm *vs* 1189 mm (Table 3.2).

Since the individuals caught on the south coast covered a restricted range of lengths and ages, the parameters estimated for this region are not likely to represent those that would have been derived if the samples had been collected from a wider range of habitats on the south coast and would thus presumably have contained larger and older fish (see Chapter 4). In this context, it is relevant that large *A. japonicus*, *i.e.* > 1000 mm, are occasionally caught in the Joint Authority Southern Demersal Gillnet and Demersal Longline Fishery, which operates in offshore waters and depths > 20 m (McAuley and Simpendorfer, 2003). Nevertheless, the von Bertalanffy growth equation provided good fits to the lengths at age of the females and males of *A. japonicus* on the south coast, as is demonstrated by the high coefficients of determination (r^2) of 0.929 and 0.930, respectively, and values for t_0 that are close to zero (Table 3.2). The lengths of females and males of *A. japonicus* on the south coast at each successive age, derived using the von Bertalanffy growth equations, indicate that growth in both sexes was similar for the first 2 years, after which it diverged, with the length of the females increasing slightly

Table 3.2. Parameter estimates derived by fitting the traditional 3-parameter and adjusted 4-parameter von Bertalanffy growth models to the lengths at age of females and males of *Argyrosomus japonicus* caught on the west and south coasts of Western Australia, including lower and upper 95% confidence limits. NA = not applicable; r^2 = coefficient of determination, n = number of fish aged.

Model	Region	Sex		L_∞	k	t_0	p	r^2	n
3-parameter	West	Females	Estimate	1213	0.274	-0.049	NA	0.930	525
			Lower	1190	0.257	-0.136	NA		
			Upper	1236	0.290	0.037	NA		
		Males	Estimate	1173	0.280	-0.087	NA	0.928	512
			Lower	1147	0.261	-0.174	NA		
			Upper	1198	0.298	0.000	NA		
	South	Females	Estimate	992	0.223	-0.509	NA	0.929	127
			Lower	782	0.143	-0.697	NA		
			Upper	1201	0.304	-0.322	NA		
		Males	Estimate	741	0.345	-0.402	NA	0.929	145
			Lower	689	0.287	-0.542	NA		
			Upper	793	0.403	-0.262	NA		
4-parameter	West	Females	Estimate	1228	0.242	0.133	0.833	0.930	525
			Lower	1198	0.205	-0.046	0.683		
			Upper	1258	0.278	0.313	0.984		
		Males	Estimate	1189	0.249	0.089	0.843	0.928	512
			Lower	1154	0.206	-0.106	0.676		
			Upper	1224	0.291	0.283	1.009		
	South	Females	Estimate	1149	0.141	-0.223	0.758	0.929	127
			Lower	259	-0.150	-0.980	0.154		
			Upper	2039	0.433	0.533	1.361		
		Males	Estimate	806	0.219	0.010	0.631	0.930	145
			Lower	672	0.057	-0.396	0.323		
			Upper	940	0.382	0.415	0.939		

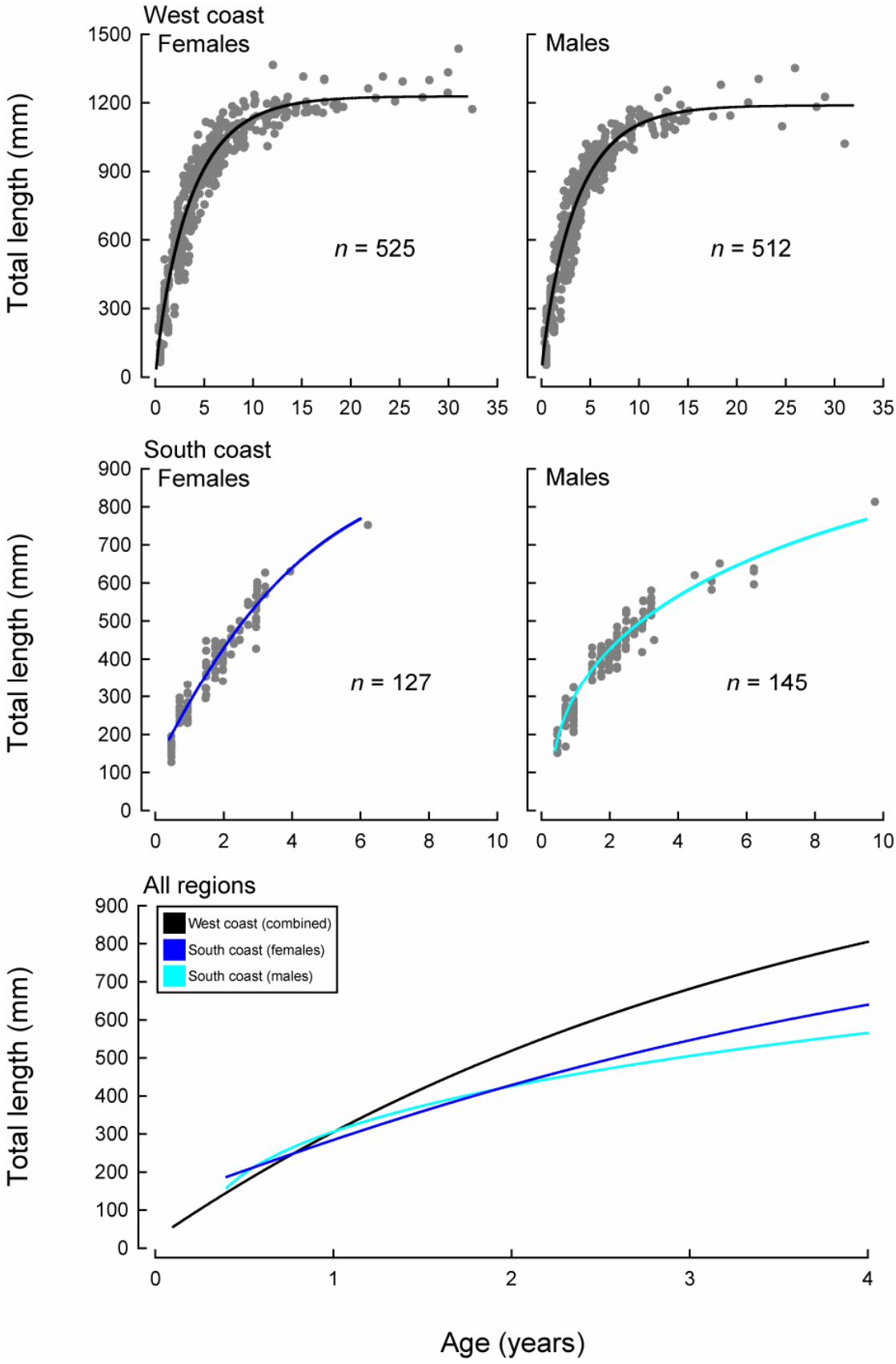


Figure 3.5. Adjusted 4-parameter von Bertalanffy growth curves fitted to lengths at age for individual females and males of *Argyrosomus japonicus* caught on the west and south coasts of Western Australia. The bottom figure compares the curves fitted using the same 4-parameter model, but with the length-at-age data truncated to 4 years of age. *n* = number of fish aged.

faster than the males (Fig. 3.5). The difference in growth between the females and males in this region was driven by significant differences in k ($p < 0.05$), as well as L_∞ ($p < 0.05$).

The *A. japonicus* caught on the south coast were exclusively collected from within an estuary and largely comprised fish ≤ four years of age. On the west coast, fish of a similar age were exclusively obtained from nearshore coastal waters together with fish covering a wide range of older ages. Once the length-at-age data on both coasts were restricted to the first four years of life, the likelihood-ratio test show that the von Bertalanffy growth equations fitted to the lengths at age of females and males on the west coast were no longer significantly different ($p > 0.05$). Thus, the data for the two sexes were pooled for this region. However, the likelihood-ratio test did demonstrate that the von Bertalanffy growth equations fitted to the lengths at age of females and males on the south coast remained significantly different ($p < 0.05$). The growth curves of both females and males on the south coast were significantly different from that derived for both sexes collectively on the west coast ($p < 0.001$). The lengths at each successive age on the west and south coasts, as derived using the von Bertalanffy growth equation, indicate that individuals in the latter of these regions grew far more slowly and particularly after 1 year of age (Fig. 3.5). Thus, by age four, the lengths of females and males on the south coast had reached 640 and 566 mm, respectively, compared with 805 mm for both sexes collectively on the west coast.

3.3.5 Relationship of total length to weight

As ANCOVA demonstrated that the regression equations that relate $\log_e$ total length (TL in mm) and $\log_e$ weight (W in g) for females and males did not differ significantly on either of the upper west, lower west or south coasts, the length-weight data for the two sexes in each region were pooled. ANCOVA further demonstrated that the length-

weight relationships did not differ between the upper and lower west coasts ($p > 0.05$). However, the length-weight relationship determined for *A. japonicus* on the west coast as a whole was significantly different from that determined for individuals on the south coast ($p < 0.05$), even when the data were restricted to include only fish of a comparable size range ($p < 0.05$). The parameter estimates for the relationship between $\log_e TL$ and $\log_e W$ for the west and south coasts are shown in Table 3.3.

Table 3.3. Parameters for the linear regression fitted to $\log_e$ total length (*TL* in mm) against $\log_e$ total weight (*W* in g), according to the equation $\log_e W = a\log_e TL + b$, of *Argyrosomus japonicus* on the west and south coasts of Western Australia, including lower and upper 95% confidence limits. MS = mean of squared residuals, r^2 = coefficient of determination, *n* = sample size. *** denotes an ANOVA *p*-value of < 0.001.

Region		Parameters		Range (mm)				
		a	b	min	max	MS	r^2	*n*
West coast	Estimate	3.007	-11.637	53	1437	0.016***	0.997	328
	Lower	2.989	-11.747					
	Upper	3.026	-11.528					
South coast	Estimate	3.068	-11.945	127	813	0.007***	0.994	272
	Lower	3.040	-12.111					
	Upper	3.096	-11.778					

3.4 Discussion

3.4.1 Growth zone deposition

The trends exhibited by the mean monthly marginal increments on sectioned otoliths of *A. japonicus* demonstrate that a single opaque zone is typically laid down annually in the otoliths of this species and that each new opaque zone becomes delineated at the edge of otoliths in November/December, *i.e.* late spring/early summer. This parallels the situation recorded for the otoliths of several other teleost species in south-western Australian waters, including Australian Herring *Arripis georgianus* (Fairclough *et al.*, 2000), Black Bream *Acanthopagrus butcheri* (Sarre and Potter, 2000), West Australian Dhufish *Glaucosoma herbraicum* (Hesp *et al.*, 2002), Goldlined Seabream *Rhabdosargus sarba* (Hesp *et al.*, 2004a) and Golden Lined Whiting *Sillago analis* (Coulson *et al*., 2005). The trends exhibited by the mean monthly marginal increments of *A. japonicus* in Western Australia also parallel those recorded for this species on the east coast of southern Africa, where this sciaenid occupies a similar latitudinal range, *i.e. ca* 20 to 40˚S (Wallace and Schleyer, 1979; Griffiths and Hecht, 1995a).

While details of the processes governing the deposition of opaque and translucent zones in fish otoliths are still poorly understood, their formation has been linked to variations in a wide range of environmental and endogenous factors, which include water temperature (Reay, 1972; Panella, 1980; Schramm Jr, 1989; Folkvord *et al*., 2004; Fey, 2006), photoperiod (Wright *et al*., 1992), feeding (Geffen and Nash, 1995), reproduction (Morales-Nin and Ralston, 1990; Mann-Lang and Buxton, 1996; Morales-Nin *et al*., 1998; Massou *et al*., 2004) and metabolism (Mina, 1968; Williams and Bedford, 1974; Kimura *et al*., 1979; Buxton and Clarke, 1989; Wright, 1991; Smith and Deguara, 2003). However, in their review, Beckman and Wilson (1995) found no clear link between a range of factors and the type of otolith zone being deposited and thus concluded that the process may be regulated by a combination of environmental

and endogenous factors, the effects of which may vary between species. Nevertheless, the marked similarity in the timing of opaque zone delineation in a number of different teleost species in the coastal waters of south-western Australia and of *A. japonicus* at a similar latitude along the coasts of two widely separate continents strongly indicate that growth zone formation is linked to consistent annual trends in one or more environmental and/or endogenous factors that are common to these species. In the context of environmental variables, it is particularly relevant that the translucent zone is formed at a time when water temperatures are increasing and thus presumably metabolism and somatic growth are increasing.

3.4.2 Length and age compositions

The length and age distributions of females were similar to those of males in all three regions, which suggests that longevity and maximum size does not differ greatly between the sexes. However, the length and age distributions of *A. japonicus* on the west and south coasts did differ markedly. Thus, in contrast to the situation on the west coast, very few fish larger than 600 mm and older than 4 years were caught on the south coast. This restricted upper size limit is not likely to be related to gear selectivity, as the same gill nets used on that coast caught *A. japonicus* with total lengths greater than 1000 mm in the Swan River in Perth. However, it is likely that *A. japonicus* with total lengths < 120 mm are present within Oyster Harbour, but the gill net mesh was not suitable for catching these smaller individuals. Nevertheless, the truncated ranges in the lengths and ages in the samples of *A. japonicus* from the south coast appear to reflect the use of that particular estuary as a nursery ground and a subsequent size and/or age-related movement out of that system. Similar size and/or age-related movements of *A. japonicus* out of estuaries have been documented in South Africa, where it has been linked to the attainment of maturity (Griffiths, 1996).

While the length and age compositions on the upper and lower west coasts were similar, the catches from the latter region comprised a greater proportion of older fish. Since the majority of the older fish on the lower west coast were obtained from recreational anglers, this may have reflected a slight bias introduced through a targeting of the larger and thus older individuals by the members of this fishing sector. This may be particularly relevant since the majority of *A. japonicus* that were collected from recreational anglers on the lower west coast were caught in the lower reaches of the Swan River Estuary, *i.e.* a known spawning ground, and during the main spawning period of this sciaenid (see Chapter 4).

The maximum total length and age recorded for *A. japonicus* during the present study were 1437 mm and 32 years, respectively. This compares with the maximum total length of 1690 mm and maximum age of 24 years recorded for this species during the study of Silberschneider and Gray (2005) in New South Wales. While that maximum age is slightly lower than that recorded in Western Australia, the majority of samples obtained during that study in New South Wales were obtained from commercial fishers. If only the samples obtained from commercial fishers in Western Australia are considered, the maximum age, *i.e.* 26 years, is then very similar to that recorded in New South Wales.

In South Africa, the maximum length and age recorded for *A. japonicus* is 1750 mm and 42 years, respectively, which are both considerably greater than has been recorded during any study of *A. japonicus* in Australia. While this disparity in both the maximum total length and age of *A. japonicus* in Australia and South Africa may reflect, in part, differences in a number of environmental characteristics, it is also likely to reflect the large genetic differences between this sciaenid in these two geographically-isolated regions (Klopper, 2005; see also Chapter 5).

3.4.3 Comparisons of growth

The results of this component of the study demonstrated that the growth of *A. japonicus* in coastal marine waters on the lower west coast, where samples were collected mainly from the coastal waters of Perth and Geraldton, is very similar to that of this species in comparable waters on the upper west coast, where samples were obtained predominantly from Kalbarri and Carnarvon/Shark Bay. Thus, this sciaenid does not follow the trend exhibited by numerous other species in the Northern Hemisphere, where growth is greater at higher than lower latitudes (*e.g*. Conover *et al*., 1997; Jonassen *et al*., 2000; McBride *et al*., 2002). However, the lack of differences in the growth of *A. japonicus* with latitude recorded in the present study parallels the lack of differences between the growth of both Tarwhine *Rhabdosargus sarba* and Yellowfin Whiting *Sillago schomburgkii* in the Perth region *vs* Shark Bay (Hesp *et al*., 2004a; Coulson *et al*., 2005). The lack of differences in the growth of each of three species at these two latitudes is perhaps surprising in view of the fact that, for example, the mean monthly water temperatures during much of the year are considerably greater at the lower of those latitudes (see Fig. 4.7). This raises the possibility that the growth of *A. japonicus* has a similar genetic basis and/or that the sum total of the environmental factors that influence growth are similar throughout the west coast. Although growth was much slower on the south than west coast, it should be recognised that the environment in which *A. japonicus* is found on those two coasts differs markedly and there is evidence that the assemblage on the south coast shows signs of inbreeding (see later in Discussion).

The growth of females and males of *A. japonicus* on the west coast is similar and particularly rapid during the first five years of life, but then slows down markedly as fish become sexually mature. The change in the pattern of growth at sexual maturity suggests that, at this time, energy resources become directed towards gonadal

development rather than mainly towards somatic growth. This pattern of change in energy allocation has been recorded for many other fish species, including some in Western Australian waters (*e.g.* Coulson *et al.*, 2005) and for other sciaenids (Beckman *et al.*, 1989; Griffiths and Hecht, 1995b), including those of *A. japonicus* in South Africa (Griffiths and Hecht, 1995a). Since the females of *A. japonicus* on the west coast attain maturity at a slightly larger size and older age than their males, *i.e.* the L_{50}s at maturity are 903 mm (*ca* 5 years) and 873 mm (*ca* 4.7 years), respectively (see Chapter 3), the lengths of females are slightly greater than those of males at all ages above the age at which males attain maturity in this region. This presumably reflects a greater selection pressure for optimising egg than sperm production (see for example Roff, 1983). The females of the sciaenids *Otolithes ruber* and *Atrobucca nibe* also grow at a slightly faster rate and attain a larger size than their males (Fennessy, 2000), as does *A. japonicus* in South African waters (Griffiths and Hecht, 1995a). A similar trend was also observed in the patterns of growth of females and males of *A. japonicus* on the south coast, but with the divergence of growth between the sexes occurring at a much smaller size and younger age. This is presumably related to the smaller size and younger age at which females and males attain maturity in this region, *i.e.* L_{50}s are 496 mm (*ca* 2.5 years) and 417 mm (*ca* 2 years), respectively (see Chapter 4).

The females and males of *A. japonicus* grow far more slowly on the south than west coasts throughout the entire range of comparable ages, which cannot be accounted for solely by the earlier attainment of maturity of individuals of the former assemblage. While the earlier maturation of *A. japonicus* on the south coast would result in a broadening of any differences between the mean length at age of individuals from each of these assemblages, particularly above 2 years of age, the fact that differences are apparent throughout their entire early life suggests other environmental or endogenous factors are contributing, during this period, to an elevation in the growth rates of those

individuals in the nearshore coastal waters of the west coast and/or to depress the growth rates of those individuals in the estuarine environment on the south coast.

Variations in life history traits, such as growth rate, may arise among populations of a species in response to differences in environmental conditions or as a consequence of selection pressures and subsequent genetic divergence (Schluter, 1996; Smith and Skulason, 1996; Agrawal, 2001). Phenotypic plasticity, *i.e.* the ability of an organism to express different phenotypes depending on the characteristics of its abiotic and/or biotic environment (Schlichting and Pigliucci, 1998; Agrawal, 2001; Sultan and Stearns, 2005), is thought to evolve in response to fluctuating environmental conditions, where phenotypic optima change spatially and temporally within and among generations (West-Eberhard, 1989; Scheiner, 1993). Since estuaries can vary greatly in their abiotic and biotic characteristics (McClusky and Elliott, 2004; Brearley, 2005), their inhabitants, such as the juvenile phases of many sciaenids (*e.g.* Cowan Jr. and Birdsong, 1985; Griffiths, 1996; Stunz *et al*., 2002), may be highly dependent on phenotypic plasticity as a means of maximising fitness in an ever-changing environment. Thus, given that the habitats utilised during the early life of *A. japonicus* on the west and south coasts differ markedly in environmental characteristics, such as food availability, water temperature, salinity and population density (Valesini *et al*., 2003; Brearley, 2005; Commonwealth of Australia, 2006; Hoeksema and Chuwen, unpubl. data), it is possible that the observed divergence in growth is due to the inherent plasticity of the life history traits of this species.

The early growth of Black Bream *Acanthopagrus butcheri* also differs markedly between estuarine populations in south-western Australia (Sarre and Potter, 2000). However, when the juveniles that had been spawned from broodstock collected from the two estuaries in which growth was most divergent were cultured under identical conditions in captivity, their growth was essentially the same (Partridge *et al*., 2003).

Thus, the disparity between the growth of individuals in the two estuaries was presumably attributable to the considerable differences that existed between the environmental characteristics of those estuaries, rather than to any potential variations in the genetic compositions of these populations.

Although the marked differences in environmental conditions of the marine waters on the west coast and the estuarine waters of the south coast are likely to have contributed to the differences in the growth rates of *A. japonicus* during their early life on these coasts, there are also a number of genetic factors that need to be taken into consideration. While the mitochondrial DNA (mtDNA) control region haplotypes of *A. japonicus* on the south coast were not genetically-distinct from those of the west coast, differences in the frequency of these haplotypes in the two regions suggest that individuals from the south coast population are reproductively isolated from those of the west coast (see Chapter 5). In view of this apparent isolation, the possibility that selection pressures have been acting on other loci cannot be discounted. As discussed in Chapter 4, there may have been selection pressures for rapid early growth and delayed maturity of *A. japonicus* on the west coast in response to a lack of suitable nursery habitat in the form of permanently-open estuaries and thus elevated levels of juvenile mortality (*e.g.* Reznick *et al*., 1990; Belk, 1995, 1998). However, since there has been limited study into the diets of those species in Western Australia that are known elsewhere to prey on nearshore coastal sciaenids, *e.g.* dolphins and sharks (Cliff *et al*., 1989; Cliff and Dudley, 1991; Ross *et al.*, 1994; de Oliviera Santos *et al*., 2002; Gannon and Waples, 2004; Barros *et al*., 2004; Bethea *et al*., 2004), the extent of this predation cannot be quantified.

Given that all of the *A. japonicus* from the south coast estuary for which sequence data were obtained shared only a single haplotype (see Chapter 5), a further genetic factor that needs to be considered is the possibility of inbreeding due to low

levels of genetic diversity. The fact that the individuals in this population exhibited numerous deformities (see Chapter 5), as well as being of poorer condition in terms of their weight at a given length (Table 3.3), indicate that the level of inbreeding might be significant. It is thus proposed that the effect of inbreeding, which has been linked with decreased rates of growth in a number of other teleost species (*e.g.* Kincaid, 1976; Winemiller and Taylor, 1982; Cena *et al*., 2006), may have also contributed to the relatively slow growth of *A. japonicus* in this estuary.

It is recognised that the apparent slower rate of growth of those *A. japonicus* in Oyster Harbour could also be attributable to the movement of faster-growing individuals out of that estuary. However, the fact that the differences in mean length at age are apparent well before the size and age at which *A. japonicus* approaches maturity in that population, which has been linked to the movement of *A. japonicus* out of similar nursery areas elsewhere (Griffiths, 1996), suggests that this is unlikely to have been the case in Oyster Harbour. Furthermore, despite the fact that *A. japonicus* mature at a similarly small size in New South Wales (Silberschneider and Gray, 2005) to those on the south coast (see Chapter 4), it has been determined that fish with lengths of 500-800 mm still maintain home ranges within particular estuarine systems (Taylor *et al*., 2006).

4.0 Habitat utilisation and reproductive biology

4.1 Introduction

4.1.1 Aspects of the reproductive biology of teleost fish

Aspects of the reproductive biology of fishes, such as spawning period and length and age at maturity, are commonly incorporated into stock assessment models, while also forming the basis for such management initiatives as the introduction of minimum legal lengths for retention and temporal and spatial closures to fishing (Hill, 1990; Hall, 1993). Furthermore, a knowledge of the spawning period of a species enables a realistic birth date to be assigned and thus facilitate the construction of sound growth curves. The approaches commonly used to determine the reproductive cycles of fish include the use of the trends exhibited throughout the year by the gonadosomatic indices (GSIs) and the prevalence of the various gonadal maturity stages and an examination of the cytological characteristics of histological sections of gonads of different developmental stages and at different times. GSIs are generally expressed as the ratio of gonad weight to body weight and the trends exhibited by this variable provide an indication of the trends exhibited by gonadal maturation throughout the year and thus also of the spawning strategy of a species. However, GSIs cannot provide a precise indication of when spawning occurs, which is generally obtained from the macroscopic staging and histological examination of gonads.

Macroscopic staging involves the allocation of gonads to a particular stage of development based solely on such external features as their size, shape and colour. The presence of yolked or hydrated oocytes in ovaries, which are typically visible through the ovarian wall, is another indicator of gonadal stage in female fish. In comparison, histological staging uses the stage of oocyte or sperm development for stages to be assigned. While macroscopic staging is the most rapid and most commonly applied, the accuracy of this method has been questioned by a number of authors (*e.g.* West, 1990; Mackie and Lewis, 2001; Walsh *et al.*, 2003). Inaccuracies may arise due to the early

stages of oocytes often not being visible through the ovarian wall and the difficulty in recognising some of the latter stages of oocyte and gonadal development, *e.g.* migratory nuclei oocytes or post-ovulatory follicles (McPherson, 1992). Furthermore, as macroscopic staging relies heavily on the experience of the observer, this technique should be supported by histology whenever possible. Histological examination of gonads is the most accurate of the available methods, but it is also the most time-consuming and it can be expensive, particularly when the large numbers of samples that are often used in reproductive studies are taken into account (West, 1990). The extent to which macroscopic and histological staging are utilised depends very much on the aims of the study, and is often a compromise between accuracy, speed and economic considerations.

Various aspects of the reproductive biology of fishes, including the timing and duration of spawning and the length and age at first maturity, are often highly variable and can differ even among assemblages of the same species. Much of this variability is due to most aspects of fish reproduction being intrinsically linked with environmental conditions, such as temperature and photoperiod (*e.g.* Bromage *et al*., 1993; Brown *et al*., 1995; Johansen *et al*., 1999; Tveiten *et al*., 2001; Migaud *et al*., 2003, 2004; Suquet *et al*., 2005; Martínez-Palacios *et al*., 2007), which can vary greatly throughout a species distribution. This may be particularly true for species that encompass a wide latitudinal range and whose populations have the potential to experience a greater array of environmental conditions. It is thus important for studies of the reproductive biology of a species to include samples from throughout their entire distribution.

4.1.2 Results of previous studies on *Argyrosomus japonicus*

While *Argyrosomus japonicus* is exploited throughout its entire Indo-Pacific distribution (Griffiths and Heemstra, 1995), detailed studies of the reproductive biology

of wild populations of this species have been conducted only in the Southern Hemisphere. However, some aspects of the reproductive biology and sound production characteristics of captive-reared *A. japonicus* have been studied in Taiwan (Lin *et al*., 1998; Ueng and Huang, 1998; Ueng *et al*., 1999; Ueng *et al*., 2007). This sciaenid is cultured in saltwater net cages in Taiwanese waters and, in this environment, both sexes mature at a total length of 700 to 800 mm and five to six years of age (Lin *et al*., 1998). However, given that fish in captivity are often kept in highly modified environments in captivity and reproduction is artificially induced, the extent to which the reproductive characteristics of *A. japonicus* recorded in these studies are accurate reflections of those of wild populations in Taiwan must be treated with caution.

In the Southern Hemisphere, aspects of the reproductive biology of wild-caught *A. japonicus* have been studied in both South Africa and Australia. Griffiths (1996) has carried out the most comprehensive study of the reproductive biology of this sciaenid in South African waters, including in his study a wide size range of individuals and samples from throughout that region. Griffiths (1996) reported that 50% of females mature at a total length of 1070 mm, *i.e.* when they are *ca* six years of age, while 50% of males are mature at 920 mm, *i.e.* when they are *ca* five years of age. Spawning takes place in the nearshore marine environment of South Africa, from August to November in the KwaZulu/Natal region, *i.e. ca* 30-31°S, and from October to January in the Southern and South-eastern Cape regions, *i.e. ca* 33-35° S (Griffiths, 1996).

Studies of the reproductive biology of Australian *A. japonicus* are sparse and have mostly involved the examination of a limited number of individuals as in South Australia (Hall, 1984, 1986; Ferguson and Ward, 2003) and previously in Western Australia (Penn, 1977; Holt, 1978). More recently, the reproductive biology of this sciaenid has been studied in New South Wales using a slightly larger sample size (Silberschneider and Gray, 2005). The latter authors reported that, in New South Wales,

50% of females mature at a total length of 679 mm, *i.e.* when they are *ca* three years of age, while 50% of males mature at 513 mm, *i.e.* when they are *ca* two years of age. Given that 53 and 33% of the mature females and males, respectively, were caught in estuarine waters during the study of Silberschneider and Gray (2005), spawning may take place in the estuarine and coastal waters of New South Wales. Fish in spawning condition were observed predominantly between November and March in New South Wales (Silberschneider and Gray, 2005). The acoustic behaviour of *A. japonicus* has been studied in the lower reaches of the Swan River Estuary in Western Australia, with this study revealing the presence of seasonal aggregations in this locality, *i.e.* from November to April (Parsons *et al*., 2006).

Studies of the fish communities in a variety of habitats in Australia (Lenanton, 1977; Anon., 1981; Chrystal, 1983; Hall, 1984, 1986; Loneragan *et al*., 1987; Gray and McDonall, 1993) and South Africa (Marais and Baird, 1980; Marais, 1981, 1983a, 1983b; Whitfield *et al*., 1994; Griffiths, 1996) have also provided further information on the distribution and abundance of *A. japonicus* throughout these regions. Griffiths (1996) reported that *A. japonicus* recruit into the turbid estuaries along the east coast of South Africa at a length of 20-30 mm and remain in the upper reaches of these systems until they have attained lengths of *ca* 150 mm. The small juveniles of *A. japonicus*, *i.e.* 150-400 mm in length, are found in the surf zone and throughout their natal estuaries, with the larger juveniles preferring the lower reaches of these systems (Griffiths, 1996). While individuals < 1000 mm in length generally do not migrate long distances, adult fish are highly migratory and move between estuaries, the surf zone and nearshore waters and depths of up to 200 m (Griffiths, 1996). While *A. japonicus* are reported to recruit into New South Wales estuaries at a similar small size as in South Africa (Silberschneider and Gray, 2005), this does not appear to be the case in Western Australia (Farmer *et al*., 2005; see also Discussion).

4.1.3 Aims

The aims of this component of the thesis, which focussed largely on *A. japonicus* on the upper and lower west coasts of Western Australia and on an estuarine assemblage on the south coast, were as follows. **1**) To elucidate the types of habitat used by *A. japonicus* at different stages in its life history. **2**) To estimate the lengths and ages at which the females and males of *A. japonicus* attain sexual maturity on the upper west, lower west and south coasts and thus be able to test the hypothesis that *A. japonicus* reaches maturity at a smaller size at the lower than higher latitudes, *i.e.* upper *vs* lower west coast. **3**) To estimate the timing and duration of the spawning period in each of the above regions and to test the hypothesis that the spawning period is longer at the lower than higher latitudes, *i.e.* upper *vs* lower west coast. **4**) To assess the spawning mode of *A. japonicus*, *i.e.* whether the species is a determinate or indeterminate spawner.

4.2 Materials and Methods

4.2.1 Laboratory procedures

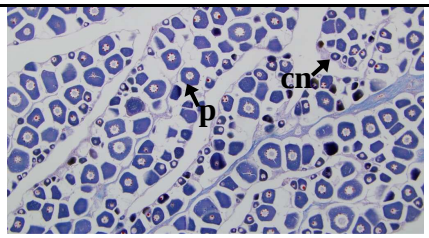
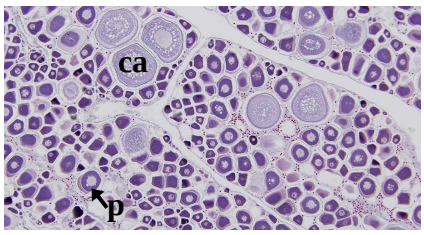
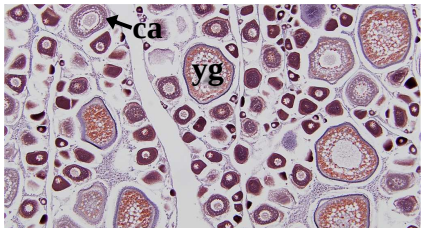
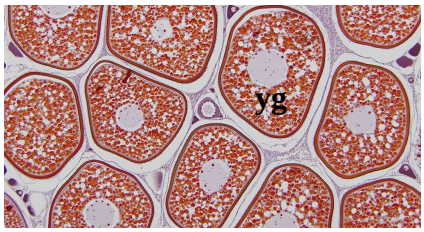
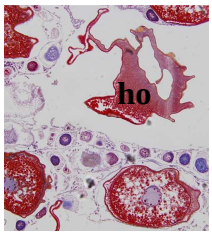
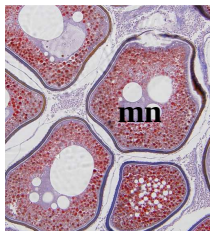
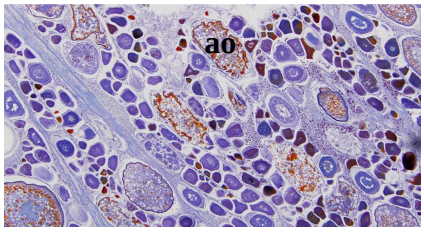
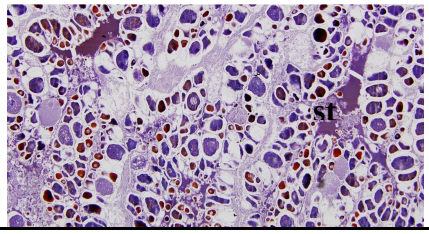
The gonads of each fish were removed and weighed to the nearest 0.01 g and then recorded macroscopically as indeterminate, *i.e.* as in the case of the gonads of small juveniles, or either as ovaries or testes. On the basis of macroscopic characteristics and the scheme outlined by Laevastu (1965), the gonads of each fish were allocated to one of the following eight stages of gonadal development; I = immature, II = resting adult, III = developing, IV = maturing, V = prespawning, VI = spawning, VII = spent, and VIII = recovering spent (Table 4.1a). The fish that possessed gonads at stages III-VIII during the spawning period were classified as mature because they had the potential to spawn, *i.e.* stages III-V, were spawning, *i.e.* stage VI, or had already spawned, *i.e.* stages VII and VIII.

In each month, the gonads of up to 20 individuals, covering a wide range of lengths and the full suite of gonadal stages observed in that month, were retained and prepared for histological examination. For this purpose, a portion of the mid-region of each ovarian or testicular lobe was placed in Bouin's fixative for *ca* 48 h (a longer period of fixation was used for the largest gonads) and dehydrated in a series of increasing concentrations of ethanol. The ovarian or testicular portions were then embedded in paraffin wax, cut transversely into 6 μm sections and stained with Mallory's trichrome. The stages in oocyte development in each section were then determined by examination using a Leica MZ7.5 dissecting microscope to validate that the stages in gonadal development assigned to each ovary on the basis of macroscopic appearance were appropriate (Table 4.1b).

Table 4.1a. Characteristics of the macroscopic stages in the development of the ovaries and testes of *Argyrosomus japonicus*. Scheme adapted from Laevastu (1965).

Stage	Ovaries	Testes
I/II *Immature/ resting*	Thin flaccid sacs that are translucent pink in colour and which occupy up to one third the length of the body cavity in early juveniles. More rounded in cross-section and pink to orange in colour, while occupying up to one half the length of the body cavity in late juveniles and resting adults. Oocytes not yet visible to the naked eye.	Threadlike and occupying up to one half the length of the body cavity in early juveniles. Larger in cross-section for late juveniles and resting adults, but still occupying up to one half the length of the body cavity. Pink to beige in colour with sperm not present in the main duct.
III *Developing*	Round in cross-section and occupying up to one half the length of the body cavity. Orange in colour and oocytes visible as tiny yellow granules.	Triangular in cross-section and occupying up to one half the length of the body cavity. Beige in colour and with sperm now present in the main sperm duct.
IV *Maturing*	Round in cross-section and occupying one half to two thirds the length of the body cavity. Opaque yellow to orange in colour with clearly discernible yolk granule oocytes throughout.	Triangular in cross-section, but now wider and deeper than in stage III and occupying one half to two thirds the length of the body cavity. Mottled beige and cream in colour with sperm now present throughout the tissue as well as in main sperm duct.
V *Prespawning*	Round in cross-section and occupying two thirds to the full length of the body cavity. Opaque yellow to orange in colour with oocytes larger than in stage IV.	Larger in cross-section and softer in texture than in stage IV, while occupying two thirds to the full length of the body cavity. Cream in colour.
VI *Spawning*	Round in cross-section and occupying two thirds to the full length of the body cavity. Yellow-orange in colour with hydrated oocytes clearly discernible.	Larger in cross-section and softer in texture than in stage V, rupturing easily when handled, and occupying two thirds to the full length of the body cavity. Cream in colour.
VII *Spent*	Slightly flaccid, but still occupying two thirds to the full length of the body cavity. Orange in colour, with some oocytes remaining, but often with red or brown tinges at the anterior end of each lobe.	Slightly shrivelled in appearance, with some sperm still present in main duct and throughout tissue, while occupying two thirds to the full length of the body cavity. Mottled-beige and cream in colour, often with brown tinges at the anterior end of each lobe.
VIII *Recovering*	Similar to stage II in diameter, but occupying one half to two thirds the length of the body cavity. Mottled red or brown in colour with a few large opaque eggs often still visible.	Flatter in cross-section and firmer in texture than in stage VII and occupying one half to two thirds the length of the body cavity. Beige in colour, sometimes with brown or red tinges as in stage VII.

Table 4.1b. Histological characteristics of the macroscopic stages in the development of the ovaries of *Argyrosomus japonicus*. Terminology for the various oocyte stages follows that outlined by Wallace and Selman (1981). Scale: 1 cm = 300 μm for all histological sections.

Macroscopic stage	Histological section	Histological characteristics
I/II *Immature/ resting*		Ovarian lamellae highly organised. Oogonia, chromatin nucleolar (cn) and perinucleolar (p) oocytes represented.
III *Developing*		Ovarian lamellae remain highly organised. Contain all previous oocyte types as well as cortical alveolar oocytes (ca).
IV *Maturing*		Cortical alveolar and yolk granule (yg) oocytes equally represented and abundant.
V *Prespawning*		Predominantly yolk granule oocytes, which are larger in diameter than in stage IV.
VI *Spawning*	 	Cortical alveolar and yolk granule vary from being abundant in early stage VI to few in late stage VI. Migratory nucleus oocytes (mn) and/or hydrated oocytes (ho) and/or post-ovulatory follicles present.
VII *Spent*		Yolk granule and cortical alveolar oocytes still present, but often undergoing atresia (ao). Spaces appear between oocytes and some scar tissue visible.
VIII *Recovering*		Scar tissue (st) abundant. Oocytes are all previtellogenic and are highly disorganised, particularly when compared with those of stage II ovaries.

4.2.2 Assessment of spawning mode

Histological sections of the mid-region of the ovaries of two prespawning individuals of *A. japonicus*, *i.e.* fish with stage V gonads, were analysed further to assess the spawning mode of this species. Using the Leica IM1000 computer imaging software (Leica Microsystems Ltd., 2001) and an image obtained via a Leica DC300 digital camera attached to a Leica MZ7.5 dissecting microscope, the circumferences of 100 randomly-selected oocytes, which had been sectioned through their nuclei, were recorded to the nearest 0.01 μm. These data were then used to calculate the diameters of those oocytes. The resultant oocyte diameter frequency distributions were then used, in conjunction with the stages of development of the oocytes, to determine whether *A. japonicus* is a determinate or indeterminate spawner *sensu* Hunter *et al*. (1985).

4.2.3 Data analyses

Logistic regression analysis was used to fit logistic curves to the probabilities that female and male fish at each specified length during the spawning period would possess gonads at one of stages III–VIII. The equation describing the probability of an individual possessing mature gonads, P, at the length, L, was $P = \{1 + e^{[-\log_e(19)(L - L_{50})(L_{95} - L_{50})^{-1}]}\}^{-1}$, where L_{50} and L_{95} are the total lengths at which 50 and 95% of the individuals, respectively, would be expected to possess gonads at stages ≥ III. On the basis of its length, the likelihood of the jth fish possessing or not possessing gonads at a stage ≥ III was calculated as P_j or $1 - P_j$, respectively. Setting X_j = 0 if the jth fish did not possess gonads at such a stage, and X_j = 1 if it did possess such gonads, the overall log-likelihood was calculated as $\sum_j \{X_j \ln P_j + (1 - X_j)\ln(1 - P_j)\}$. The logistic equation was fitted by maximizing this log-likelihood, using SOLVER in Microsoft Excel. The data were randomly resampled and analysed to create 1000 sets of bootstrap estimates of the parameters of the logistic equation and of the probabilities of

females and males being mature for each of a range of specified lengths. The 95% confidence limits of the probability of maturity at each specified length were taken as the 2.5 and 97.5 percentiles of the corresponding predicted values resulting from this resampling analysis. The medians of the bootstrap estimates were used as the point estimates of each parameter and of the probability of maturity at each specified length. The logistic regressions describing the length at maturity data for each water body were compared using the likelihood ratio test outlined in Chapter 3.

The gonadosomatic index (GSI) was calculated separately for each female and male fish using the equation GSI = $W1/(W2 - W1) \times 100$, where *W1* = the wet weight of the gonad, *W2* = the total wet weight of the fish and thus *W2 – W1* = somatic weight. The index was calculated using data for fish ≥ the estimated L_{50} at first maturity for females and males. The mean GSIs for each bimonthly interval, *i.e.* June-July, August-September, October-November, December-January, February-March, April-May, were calculated and plotted and used to estimate the duration of the spawning period and the time of peak spawning.

4.2.4 Water temperature

On the upper west coast, mean monthly water temperatures were obtained for both Carnarvon and Kalbarri. The mean monthly water temperatures for Carnarvon were calculated from measurements recorded by the Western Australian Department of Fisheries between 1998 and 2005 at a depth of *ca* 12 m at Uraine Bank on the eastern side of Dorre Island (25° 17'S, 113° 13'E), *i.e.* a locality near to which the majority of those commercial samples of *A. japonicus* examined from this region were caught. The mean monthly water temperatures for Kalbarri, which were provided by CSIRO, were calculated from measurements recorded between 1984 and 1991 at a depth of *ca* 5 m at a locality *ca* 80 km south of the Murchison River mouth (28° 23'S, 113° 13'E). Water

temperatures for the lower west and south coasts were again provided by the Western Australian Department of Fisheries. On the lower west coast, mean monthly water temperatures were calculated from measurements recorded between 2001 and 2005 at *ca* 1 m below the surface near the entrance of the Swan River Estuary in Cockburn Sound. Mean monthly water temperatures for the south coast were calculated from measurements recorded between 1996 and 2007 at the surface of the water column at Emu Point, *i.e.* the mouth of the Kalgan River/Oyster Harbour.

4.3 Results

4.3.1 Habitat utilisation

The length-frequency data for fish caught in all regions and regardless of method indicate that small juvenile *A. japonicus* typically reside in nearshore waters and depths < 10 m (Fig. 4.1). However, the larger, mature individuals on the west coast were caught in both these nearshore waters and in offshore waters and up to 200 m in depth (Fig. 4.1). On the lower west coast, adult *A. japonicus* were most common in nearshore waters during the spawning period, *i.e.* November to April, and were more prevalent in offshore waters and particularly in depths of 80 to 110 m water offshore at other times (B. Farmer, pers. obs.). The length-frequency distribution of *A. japonicus* in offshore waters produced a distinct modal class of 900-999 mm and thus the majority have a total length > L_{50} at first maturity (Fig. 4.1).

During sampling, it became apparent that the small juveniles of *A. japonicus*, *i.e.* fish < 400 mm, occupied very different nearshore habitats on the west and south coasts. For example, while small juveniles of *A. japonicus* were caught predominantly in nearshore coastal waters in the Carnarvon and Geraldton regions, where there are few or no estuaries, and were rarely caught in estuaries further south on the west coast, individuals of a similar size were caught in the estuarine environment of Oyster Harbour on the south coast. The length-frequency distribution of *A. japonicus* caught by seine netting in nearshore waters of the west coast contained a distinct modal class of 80-99 mm, while that for fish taken by line ranged from 180 to 399 mm and had no conspicuous mode (Fig. 4.2). The length-frequency distribution for *A. japonicus* caught by gill netting on the south coast produced a continuous distribution of 120-399 mm, but with two distinct modal classes of 260-279 mm and 380-399 mm (Fig. 4.2).

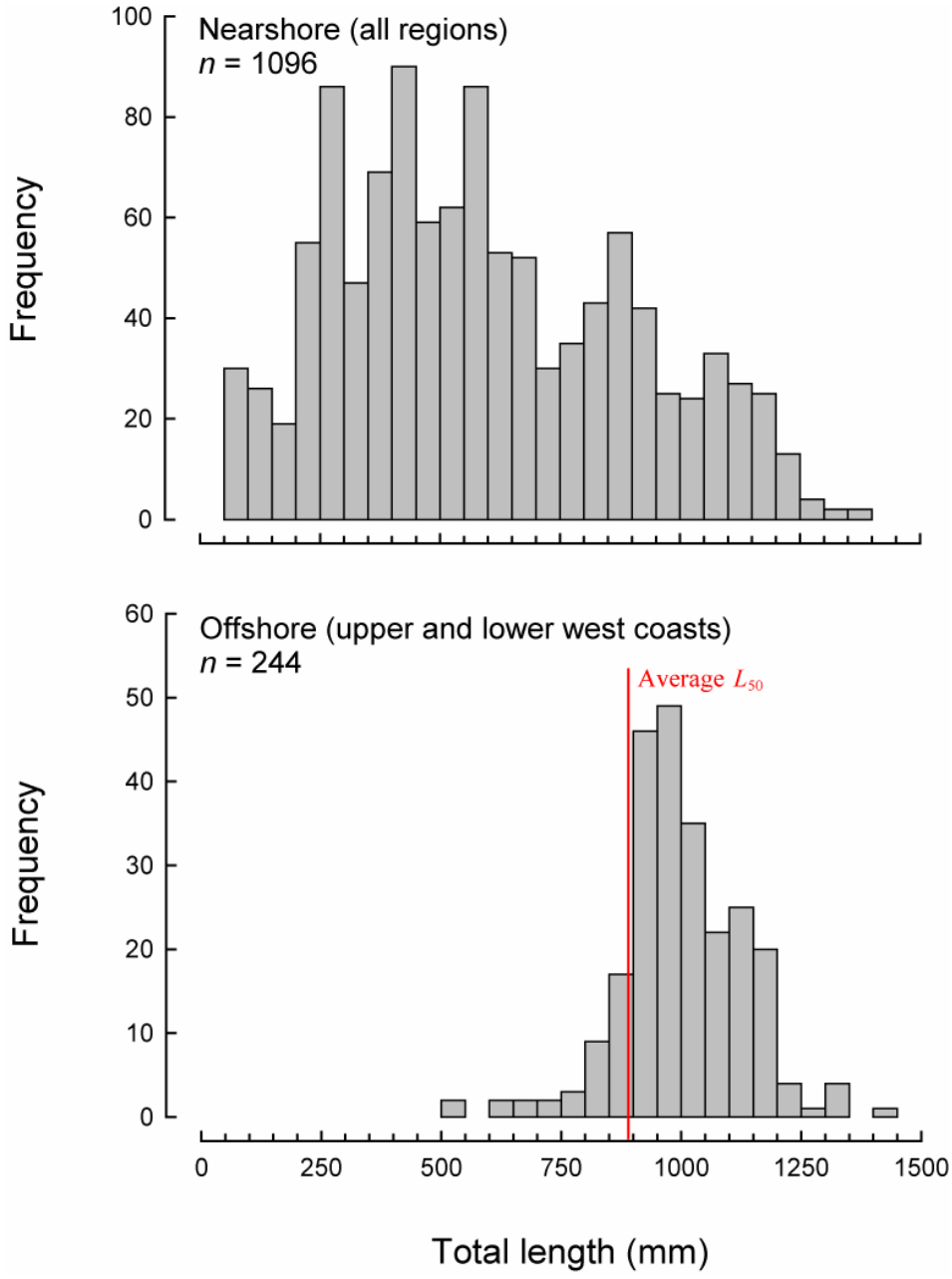


Figure 4.1. Length-frequency histograms for *Argyrosomus japonicus* caught in nearshore waters, *i.e.* coastal or estuarine waters <10 m deep, of all regions, and those caught in offshore waters, *i.e.* depths >20 m, of the west coast of Western Australia. *n* = sample size. The average L_{50} for females and males is shown.

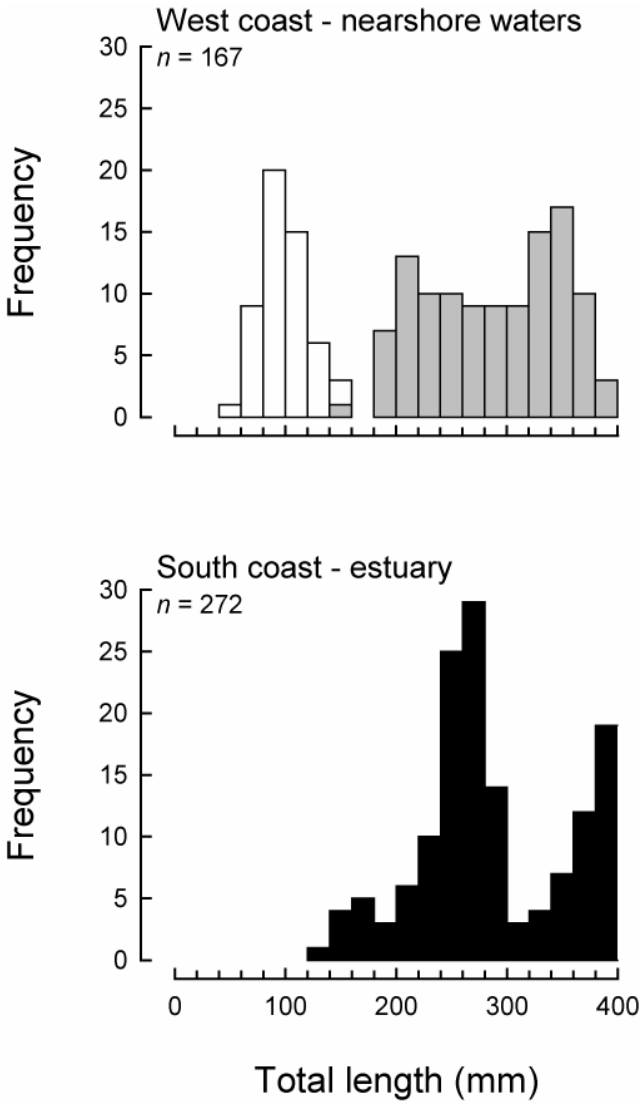


Figure 4.2. Length-frequency histograms for small juvenile *A. japonicus*, *i.e.* fish < 400 mm, caught in nearshore coastal waters on the west coast and from an estuary on the south coast. Histogram colour denotes capture method, *i.e.* white = seine net, grey = hook and line, black = gill net.

4.3.2 Lengths and ages at maturity

The data used for determining the lengths and ages at which *A. japonicus* attains maturity on each of the upper west, lower west and south coasts were pooled for those months considered to correspond to the main spawning period in each of these regions. This period was designated as May to September on the upper west coast, October to March on the lower west coast and from at least November to February on the south coast, *i.e.* where sampling was conducted only seasonally (see Section 4.3.3). The likelihood-ratio test demonstrated that the logistic curves relating length and the probability that an individual is mature for females and males were significantly different on each of the upper west ($p < 0.01$), lower west ($p < 0.01$) and south ($p < 0.001$) coasts and thus, data for each sex were analysed separately in all regions. Since the likelihood-ratio test further demonstrated that the logistic curves relating length and the probability that an individual is mature for females and males on the upper west coast did not differ significantly from those for the corresponding sexes on the lower west coast ($p > 0.05$), these data were pooled. However, the likelihood-ratio test demonstrated a significant difference between the logistic curves relating length and the probability that an individual is mature for females and males on both the west and south coasts ($p < 0.001$), and thus the data for the two sexes on each of those coasts were analysed separately.

All females and males of *A. japonicus* caught on the west coast with total lengths < 800 mm were immature, *i.e.* possessed gonads at stages I-II (Fig. 4.3). Fish with mature gonads, *i.e.* stages III-VIII, were first found in the 800-849 mm length class and all females and males had attained maturity by the time they had reached a total length of 1050 and 1000 mm, respectively (Fig. 4.3). The L_{50} at first maturity was greater for females than males, *i.e.* 903 *vs* 873 mm (Table 4.2). On the south coast, females and males with mature gonads first appeared in the 450-499 mm and 400-

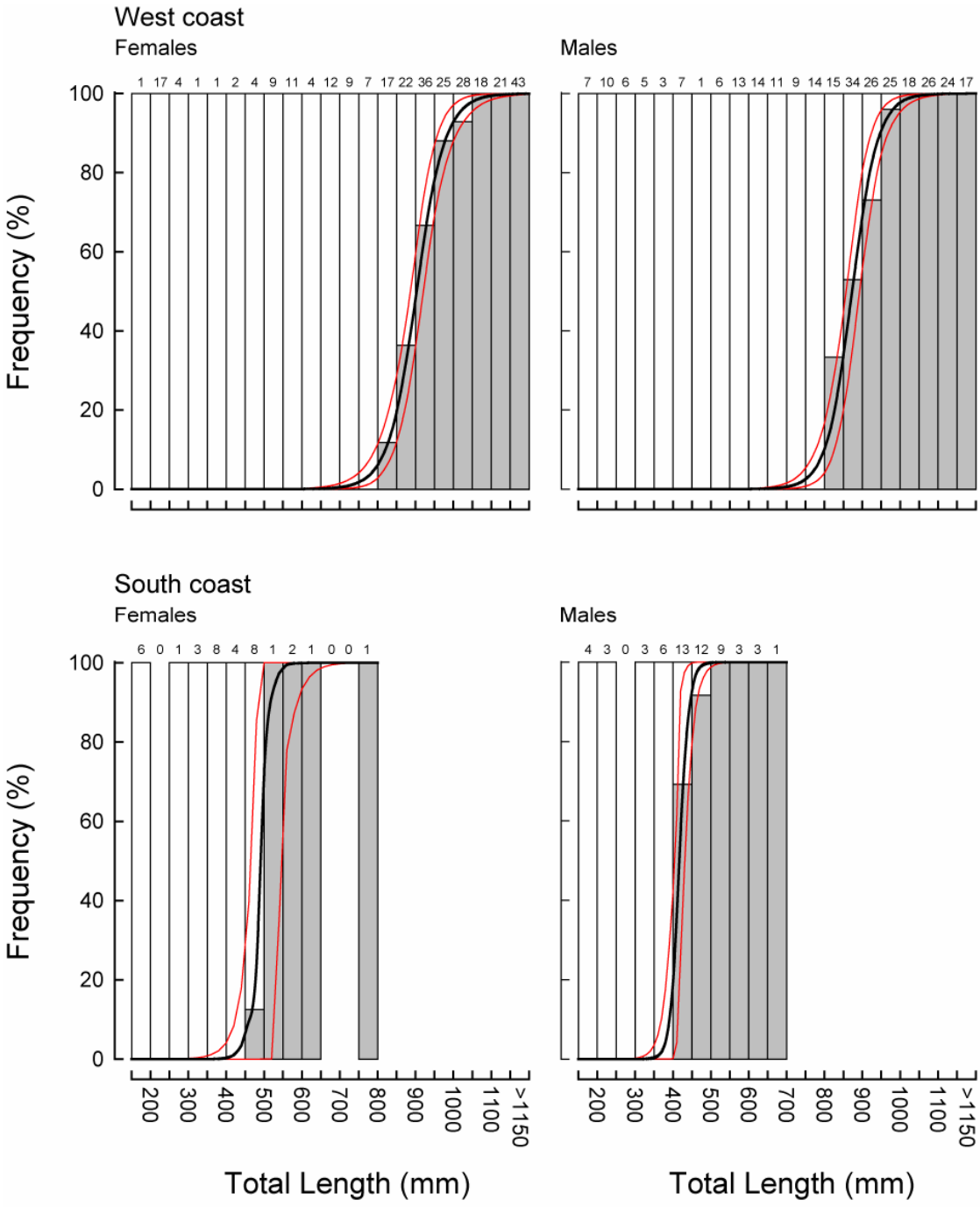


Figure 4.3. Percentage frequencies of occurrence of fish caught during the spawning period with ovaries or testes at stages III-VIII in sequential 50 mm length classes of *Argyrosomus japonicus* on the west and south coasts of Western Australia. In each case, the logistic curves (black line) and their 95% confidence limits (red lines) were derived from a logistic regression analysis that described the relationship between total length and the probability that an individual possessed gonads at stages III-VIII. Sample sizes of fish in each length class are shown.

449 mm length classes, respectively, and all females and males were mature by the time they had reached a total length of 500 mm (Fig. 4.1). The L_{50} at first maturity of females was greater than that of males, *i.e.* 496 *vs* 417 mm (Table 4.2). Furthermore, the L_{50}s for both females and males on the west coast were far greater than those of the corresponding sexes on the south coast (Table 4.2). Indeed the lower limits of the 95% confidence intervals for the L_{50} for females and males on the west coast far exceeded the upper limit of the 95% confidence intervals for the corresponding sexes on the south coast.

Table 4.2. Estimates of lengths (mm, TL) at maturity, L_{50} and L_{95}, of *Argyrosomus japonicus* on the west and south coasts and their lower and upper 95% confidence limits. *n* = sample size.

Region	**Sex**		L_{50}	L_{95}	***n***
West coast	Females	Estimate	903	1015	291
		Lower	886	983	
		Upper	921	1045	
	Males	Estimate	873	973	292
		Lower	857	945	
		Upper	893	997	
South coast	Females	Estimate	496	530	37
		Lower	466	488	
		Upper	541	610	
	Males	Estimate	417	454	57
		Lower	404	422	
		Upper	431	475	

On the west coast, maturity had been attained by a few *A. japonicus* by four years of age, while over half of the females and males caught at the end of their sixth, seventh and eighth years of life and all older individuals were mature (Fig. 4.4). On the south coast, females and males of *A. japonicus* attained maturity at a much younger age than the corresponding sexes on the west coast. In this region, the females of *A. japonicus* first attained maturity by the end of their third year of life and all were mature by four

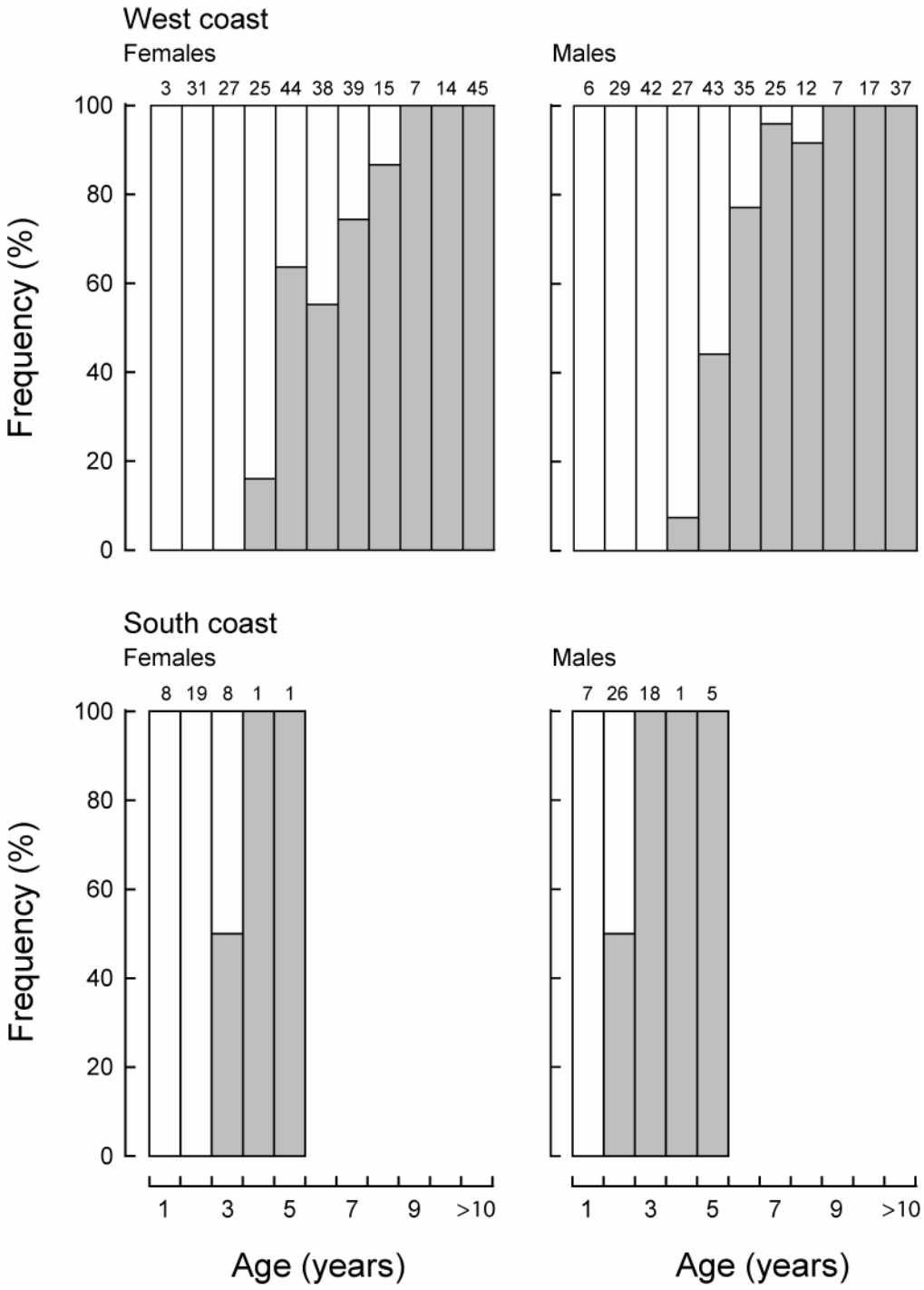


Figure 4.4. Percentage frequencies of occurrence of fish caught during the spawning period with ovaries or testes at stages III-VIII in sequential age classes of *Argyrosomus japonicus* on the west and south coasts of Western Australia. Sample sizes of fish in each age class are shown.

years of age, while maturity was first attained by the males at the end of their second year of life and all were mature by three years of age (Fig. 4.4).

4.3.3 Spawning period

On the upper west coast, the females of *A. japonicus* with total lengths $\geq L_{50}$ at first maturity and containing resting ovaries, *i.e.* stage II, were most abundant between October and March (Fig. 4.5). While females of *A. japonicus* with ovaries at stages III-IV were present throughout much of the year, they were most prevalent in April/May. Females of *A. japonicus* with ovaries at stages V-VI (prespawning or spawning) were also present in most months of the year, but were most prevalent in June/July. In August and September, the ovaries of the majority of females were at stage VIII (recovering) (Fig. 4.5). The bimonthly trends in both the prevalence of the different gonad stages and GSIs for males of *A. japonicus* on the upper west coast that had total lengths $\geq L_{50}$ at first maturity showed that, as for the females, males with testes at stages III-IV and V-VI were present in all months of the year (Fig. 4.5). Since the mean bimonthly GSIs for females and males on the upper west coast did not follow a consistent trend, they are not joined by a line in Figure 4.5.

On the lower west coast, the females of *A. japonicus* that had total lengths $\geq L_{50}$ at first maturity and possessed stage II ovaries were most abundant between June and September (Fig. 4.5). Females of *A. japonicus* with ovaries at stages III-IV were first found in October while those with ovaries at stages V-VI were first recorded in November. While fish with prespawning or spawning ovaries were present from November to April, they were the most prevalent category from November to January. By February and March, the ovaries of the majority of females were at stage VIII (Fig. 4.5). Although the bimonthly trends exhibited by the frequency of different stages in the gonadal development of the males of *A. japonicus* with total lengths $\geq L_{50}$ at first

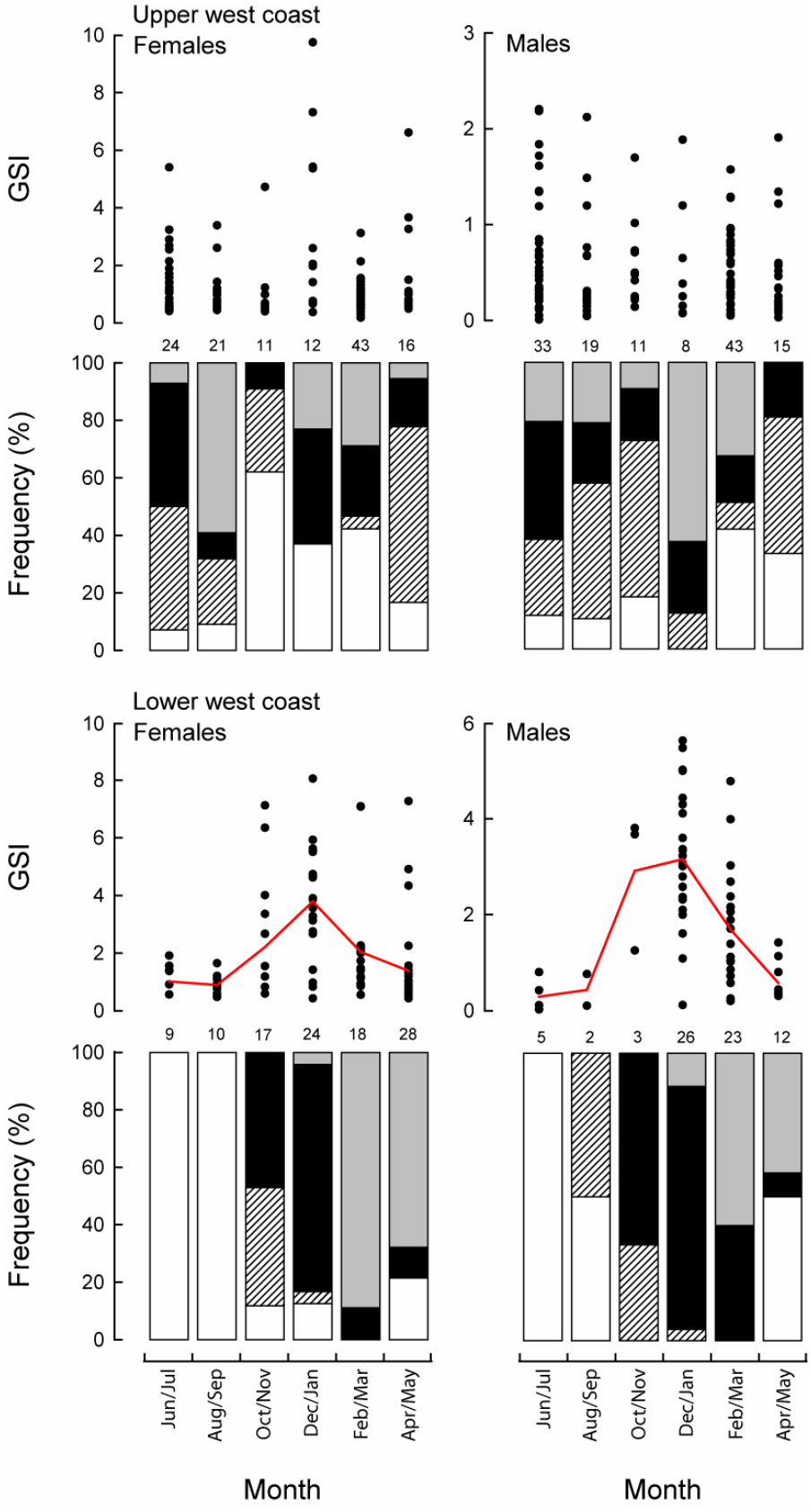


Figure 4.5. Gonadosomatic indices for individual *Argyrosomus japonicus* and percentage frequencies of stage II (□), stage III/IV (▨), stage V/VI (■) and stage VII/VIII (▩) gonads of females and males that had lengths greater than their L_{50} at first maturity and were caught in each 2-month interval on the upper west and lower west coasts. The red line, when shown, represents the mean of the individual GSIs.

maturity were similar to those just described for females, males with testes at stages III and IV were first collected in September (Fig. 4.5). The mean GSIs of female *A. japonicus* caught on the lower west coast remained at < *ca* 1 from June to October and then rose to a peak of *ca* 4 in December/January, before declining to < *ca* 2 in February/March and *ca* 1.5 in April/May (Fig. 4.5). While the mean bimonthly GSIs of male *A. japonicus* caught in the same waters follow a very similar trend, the GSI rises in October/November to a higher annual maximum than that of females (Fig. 4.5).

On the south coast, all female *A. japonicus* that were caught in August, February and May and had total lengths $\geq L_{50}$ at first maturity possessed stage II ovaries (Fig. 4.6). Females of *A. japonicus* with ovaries at stages V-VI were recorded only in November (Fig. 4.6). All of the males caught in August and May that had total lengths greater than their L_{50} at first maturity, possessed stage II testes (Fig. 4.6). The majority of the males caught in November and *ca* 35% of those caught in February had stage V-VI testes, with the majority (53%) of males caught in the latter month having stage VII or VIII testes (Fig. 4.6). The mean GSIs of female *A. japonicus* caught on the south coast in February, May and August remained between 0.5 and 1, with a distinct peak of *ca* 3.5 in November (Fig. 4.6). While the mean GSIs of male *A. japonicus* caught in the same waters followed a similar trend, the peak in November was slightly lower, *i.e. ca* 2.5, and remained relatively high in February (Fig. 4.6).

4.3.4 Water temperatures

Mean monthly water temperatures at Carnarvon on the upper west coast rose progressively from *ca* 21.5°C in October to reach a maximum of *ca* 25°C in February to April, before declining precipitously to *ca* 21°C in June to September (Fig. 4.7). While the mean monthly water temperatures for Kalbarri followed a similar trend to that described for Carnarvon, the maximum and minimum temperatures were *ca* 0.5 and 2°C

lower, respectively (Fig. 4.7). Mean monthly water temperatures off Perth on the lower west coast rose progressively from *ca* 15.5°C in July to reach a maximum of *ca* 24°C in January, before declining precipitously to *ca* 16.5°C in June (Fig. 4.7). The trend exhibited by the mean monthly water temperatures at Albany on the south coast was similar to that described for Perth, but with maximum and minimum temperatures that were *ca* 1 and 3.5°C lower, respectively (Fig. 4.7).

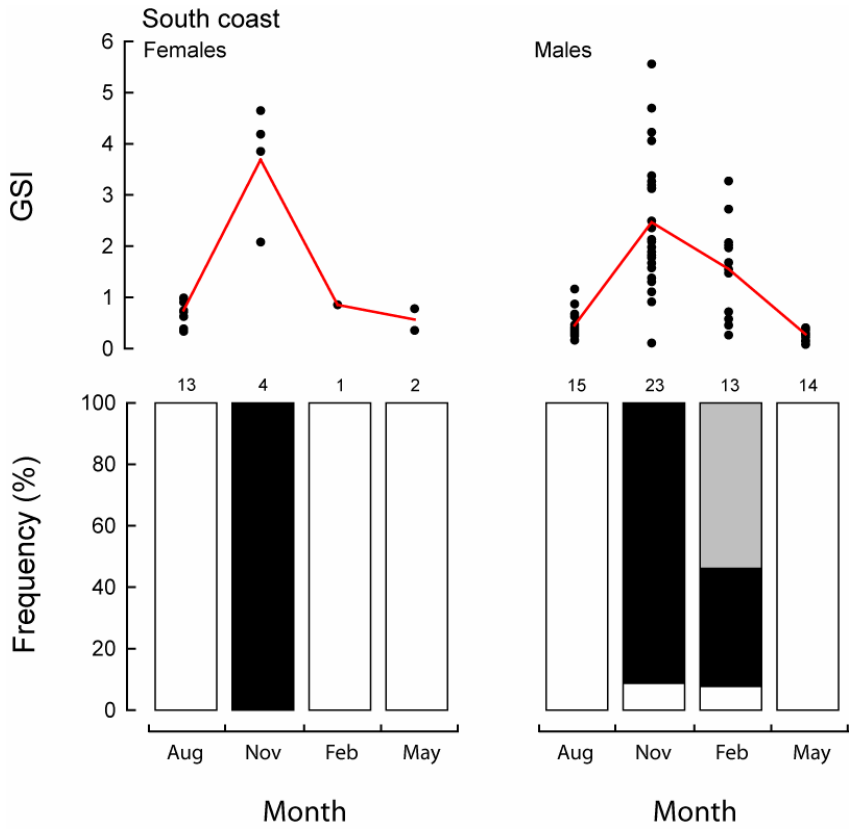


Figure 4.6. Gonadosomatic indices for individual *Argyrosomus japonicus* and percentage frequencies of stage II (□), stages V/VI (■) and stages VII/VIII (▨) gonads of females and males that had lengths greater than their L_{50} at first maturity and were caught seasonally on the south coast. The red line represents the mean of the individual GSIs.

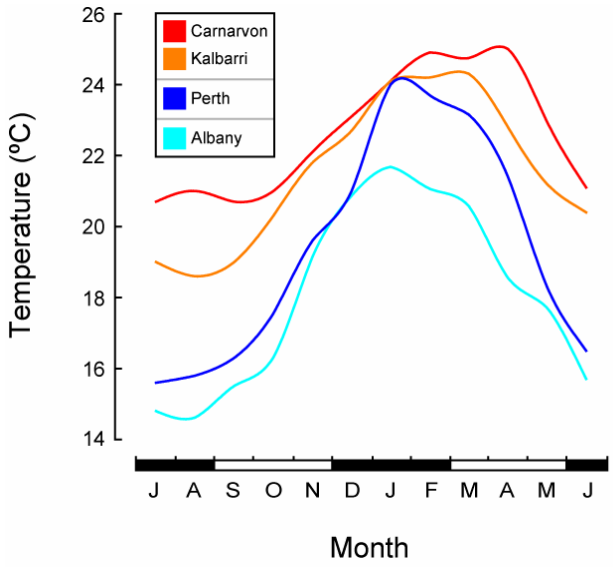


Figure 4.7. Mean monthly water temperatures for Carnarvon and Kalbarri on the upper west coast, Perth on the lower west coast and Albany on the south coast. On the x-axis, closed rectangles represent the summer and winter months and open rectangles the autumn and spring months.

4.3.5 Spawning mode

The diameter frequency distributions for oocytes in the ovaries of two female *A. japonicus* collected during the spawning period produced a prominent modal class at 40-59 µm (Fig. 4.8), which represented oocytes at the chromatin nucleolar and perinucleolar stages. There was also a group of oocytes with diameters that lay mainly in the range of 340-419 µm and which, in one of the ovaries, produced a modal class of 380-399 µm that represented predominantly yolk granule oocytes. As the oocytes with intermediate diameters were always cortical alveolar oocytes, the ovaries of each fish contained all oocyte stages between the chromatin nucleolar and yolk granule stages. This accounts for the oocyte diameters of each of the two fish forming a largely continuous overall distribution (Fig. 4.8).

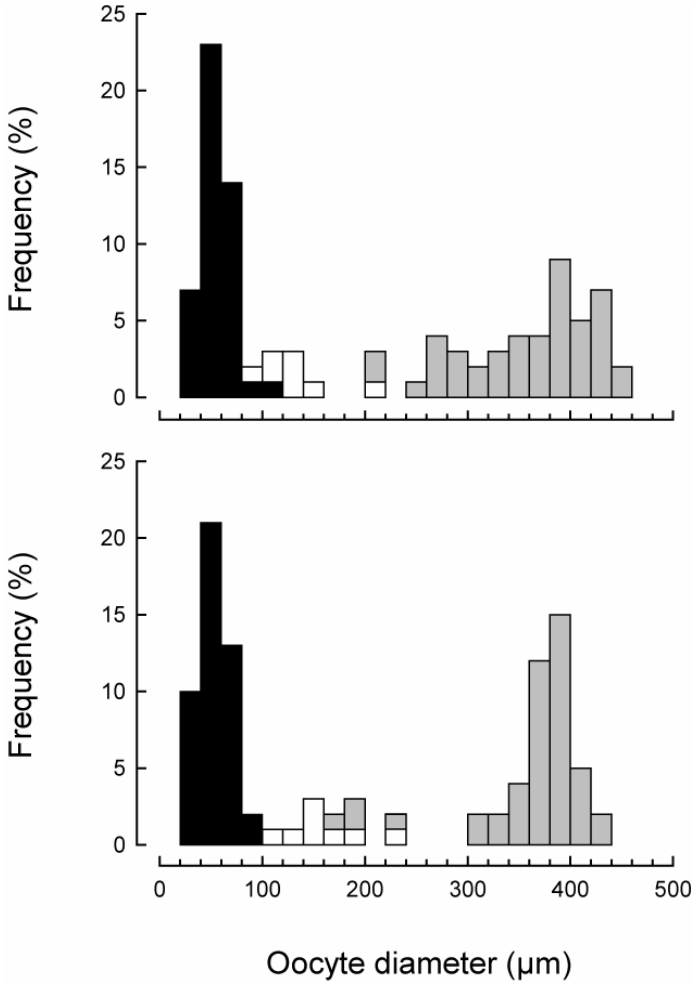


Figure 4.8. Oocyte diameter frequency distributions for stage V (prespawning) ovaries of two *Argyrosomus japonicus*. Black bars refer to chromatin nucleolar and perinucleolar oocytes, white bars to cortical alveolar oocytes and grey bars to yolk granule oocytes.

4.3.6 Evidence of spawning in the Swan River Estuary

Despite advertising throughout the year for recreational anglers in the Swan River Estuary to donate the filleted frames of any *A. japonicus* they had retained, such frames were recovered only for fish caught in Mosman Bay, *i.e.* in the lower reaches of that estuary, between late October and April (Fig. 4.9). The willingness of anglers to help thus indicates that *A. japonicus* was present only or predominantly during those months. Furthermore, *A. japonicus* was only caught during my sampling trips to Mosman Bay between November and January (Fig. 4.9), which corresponds to the main spawning period of this sciaenid on the lower west coast. Despite using a range of different rigs at this locality, including hooks used to catch the small juveniles of *A. japonicus* elsewhere (see Chapter 2), none of the individuals caught either on those trips or were caught and donated by recreational anglers had total lengths < L_{50} at first maturity (Fig. 4.9). In addition, passive acoustic recordings taken from Mosman Bay, *i.e.* the lower reaches of the Swan River Estuary, confirmed that substantial numbers of *A. japonicus* were present in this locality between November and February and some remained in the area until April (Parsons *et al.*, 2006).

Hydrated oocytes and post-ovulatory follicles (POFs) with the same characteristics as those described for newly-formed POFs, *i.e.* < 6 h old, in other fish species (Hunter & Macewicz, 1985), were found in the ovaries of three of the female *A. japonicus* caught in Mosman Bay during the spawning period. The presence of numerous hydrated oocytes in the ovarian ducts of these three fish indicate that ovulation was occurring (Fig. 4.10). As with other teleosts, the hydrated oocytes of *A. japonicus* collapsed on sectioning (Fig. 4.10), while the thecal and granulosa cells of the newly-formed POFs produced convoluted folds and the nuclei of these cells stained darkly and were well aligned.

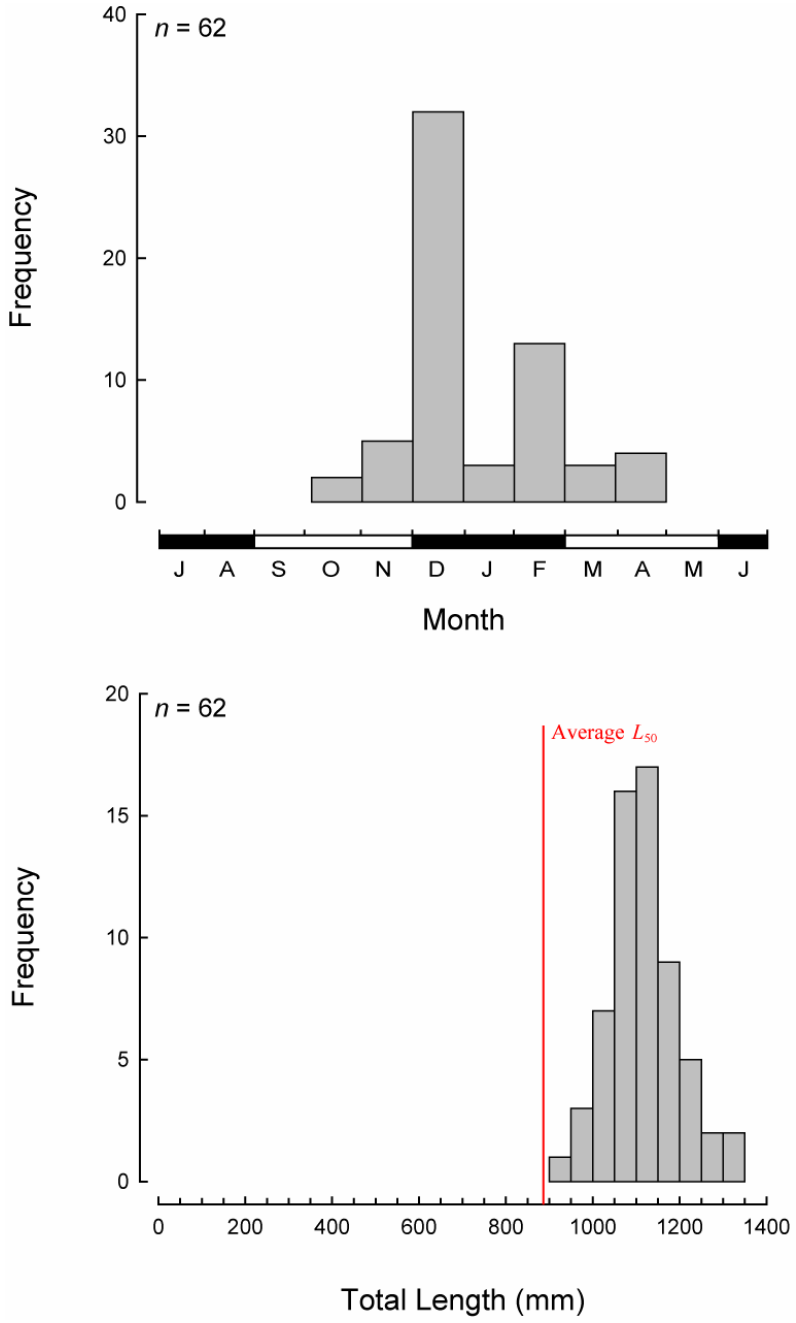


Figure 4.9. (a) Monthly catches of *Argyrosomus japonicus* collected from recreational anglers and during sampling excursions in Mosman Bay, *i.e.* the lower reaches of the Swan River Estuary, and (b) the length-frequency distribution for all fish caught in this locality. The average L_{50} for females and males is shown.

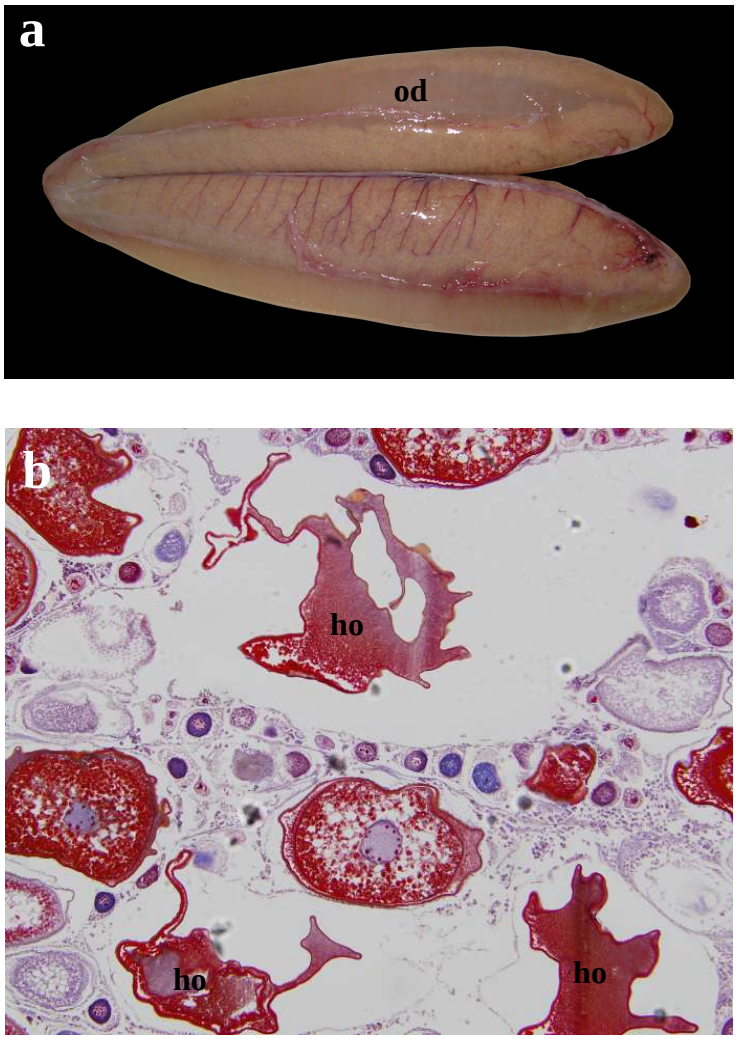


Figure 4.10. (a) Stage VI ovary from one of the female *Argyrosomus japonicus* caught in the lower reaches of the Swan River Estuary that was undergoing ovulation at the time of capture. Note the hydrated oocytes in the ovarian duct, od, which appears more translucent than the surrounding tissue. Scale: 1 cm = 3 cm. (b) Histological section of the same ovary showing hydrated oocytes, ho. Scale: 1 cm = 150 μm.

4.4 Discussion

4.4.1 Habitat utilisation

The juveniles of *A. japonicus*, *i.e.* individuals with lengths < L_{50} at first maturity, were caught almost exclusively in nearshore waters < 10 m deep, while the larger adults were caught in the same nearshore waters as well as in offshore waters, *i.e.* waters > 20 m deep, and depths up to 200 m. The lack of juvenile *A. japonicus* in catches obtained from deeper waters is not a consequence of gear selectivity because identical hook sizes and rigs were used to sample these waters as nearshore waters, where this method yielded substantial numbers of juvenile fish. While the small juveniles were caught exclusively in nearshore waters < 10 m deep, they were mainly encountered in coastal waters and particularly in protected embayments and along long-energy beaches on the west coast and in a single estuary on the south coast. The small juveniles of *A. japonicus* are most commonly found in the estuaries of New South Wales and South Africa, which are thus regarded as containing their main nursery habitats (Gray and McDonall, 1993; Griffiths, 1996; Silberschneider and Gray, 2005).

The greater use of nearshore coastal waters as nursery areas by *A. japonicus* on the west coast of Australia is almost certainly related to the physical characteristics of that coastline. The ridge of submerged barrier reefs and islands present at distances of 3 to 10 km offshore along much of the west coast of Australia, provides the nearshore waters of that coast with considerable shelter from offshore wave conditions (Masselink and Pattiaratchi, 2001; Valesini *et al.*, 2003). In addition, large amounts of macrophytic detritus are often present along this coast, which provides habitat and food for juvenile fish in this relatively sheltered zone (Lenanton, 1982). In contrast, the coastlines of the south coast of Western Australia, New South Wales and South Africa are dominated by higher-energy wave regimes (Chapman *et al.*, 1982; Fennessey, 2000; Commonwealth of Australia, 2006). As there is a paucity of permanently-open estuaries on the west

coast, particularly north of Perth (Potter and Hyndes, 1999; see also Chapter 2), the lack of a connection between these estuaries and the oceanic waters in which this species predominantly spawns would further limit the opportunities for the recruitment of juvenile *A. japonicus*.

While small juvenile *A. japonicus* have been caught in a few west coast estuaries during previous studies (Holt, 1978; Chrystal, 1983; Potter *et al*., 1983), they were never abundant in these systems. For example, extensive trawling of the Swan River Estuary on 67 sampling occasions over 6 years never yielded 0+ *A. japonicus*, while only 41 post 0+ individuals were caught over this same period (Chrystal, 1983). While Holt (1978) caught some 0+ and 1+ *A. japonicus* in the Swan River Estuary, fish of similar ages were encountered in comparable abundances in the nearby coastal waters. When encountered in estuaries on the west coast, juvenile *A. japonicus* were generally > 150 mm in total length. This differs greatly from the situation in eastern Australia and South Africa, where this sciaenid recruits at a much smaller size, *i.e.* 20-30 mm (Griffiths, 1996; Silberschneider and Gray, 2005). The recruitment of *A. japonicus* to estuaries in these regions has also been linked with periods of freshwater outflow, which it has been hypothesised assists the young juveniles to locate such systems (Griffiths, 1996). On the lower west coast of Australia, the spawning period of *A. japonicus* coincides with the driest months of the year, at least 4-5 months before any consistent rainfall (Sturman and Tapper, 1996; Brearley, 2005). Thus, recruitment of *A. japonicus* to the few permanently-open estuaries present along this coast may not occur until the start of winter and freshwater discharge starts flowing into the marine environment, *i.e.* when such individuals are *ca* 150 mm in length (see Chapter 3).

While the large adults of *A. japonicus* were caught throughout all sampled environments, there appeared to be a definite seasonality to their movements. For example, adult *A. japonicus* were most commonly encountered in nearshore waters

during the summer months, while they start to appear in the catches of charter boats fishing in *ca* 100 m water offshore Perth during May and are most prevalent in this environment during winter (B. Farmer, pers. obs.; A. Bevan, Shikari Charters, pers. comm.). There is also strong anecdotal evidence of large adult *A. japonicus* being caught by recreational anglers in the nearshore zone during winter, but only when there is extremely rough weather. This pattern of catches suggests that the movement of adult *A. japonicus* between nearshore and offshore waters, at least on the lower west coast, is closely linked to their spawning period and possibly also feeding-related movements during periods of high seas. The movement of adult *A. japonicus* into rivers and estuaries appears to be further linked to an absence of freshwater outflow, with adult fish preferring marine waters and only venturing appreciable distances into these systems during the dry summer months when salinities correspond to those of full strength seawater (Holt, 1978; Loneragan *et al*., 1989; B. Farmer, pers. obs.). Similar seasonal movements of adult *A. japonicus* have been documented in South Africa (Smale, 1985; Griffiths, 1996).

4.4.2 Lengths and ages at maturity

The results of this component of the thesis demonstrated that the length at maturity of *A. japonicus* in coastal marine waters on the lower west coast, where samples were collected mainly from the coastal waters of Perth and Geraldton, is very similar to that of this species in comparable waters on the upper west coast, where samples were collected mainly from Kalbarri and Carnarvon/Shark Bay. Thus, this sciaenid does not follow the trend exhibited by numerous other species in which the length at maturity is greater at higher than lower latitudes (*e.g*. Richards *et al*., 1990; Sampson and Al-Jufaily, 1999; Abookire and Macewicz, 2003). However, the similarity in the length at

maturity of *A. japonicus* on the upper and lower west coasts parallels the lack of a significant difference in the growth of this species throughout that same region.

The females of *A. japonicus* on both the west and south coasts mature at a slightly greater length and age than their males, which parallels the situation with several other sciaenids (*e.g.* Cisneros-Mata *et al.*, 1995; Hutchings *et al*., 2006), including South African *A. japonicus* (Griffiths, 1996). This presumably reflects a greater selection pressure for optimising egg than sperm production (see Roff, 1983). However, the females and males of *A. japonicus* on the west coast mature at a much larger size and older age than the corresponding sexes on the south coast. For example, the L_{50}s for females and males of *A. japonicus* on the west coast were 903 and 873 mm, respectively, while those for the corresponding sexes on the south coast were only 496 and 417 mm, respectively. Thus, the L_{50}s for females of *A. japonicus* on the west and south coasts are *ca* 74 and 43% of the L_{∞}, respectively.

The large disparity in L_{50}s for *A. japonicus* on the west and south coasts may have arisen solely due to differences in environmental conditions or as a consequence of selection pressures and subsequent genetic divergence. Variation in life history traits due solely to differences in the abiotic or biotic environment is often referred to as phenotypic plasticity (Schlichting and Pigliucci, 1998; Agrawal, 2001; Sultan and Stearns, 2005). Since the locations sampled on the west and south coasts differ markedly in a wide variety of environmental characteristics, including population density and water temperatures (Valesini *et al.*, 2003; Brearley, 2005; Commonwealth of Australia, 2006; Hoeksema and Chuwen, unpubl. data), these may be acting alone to influence the very different expression of phenotype on either of these coasts.

Although the considerable differences in environmental characteristics of the west and south coasts are likely to influence phenotype, there are a number of genetic factors that also need to be considered. While the mtDNA control region haplotypes of

A. japonicus on the south coast were not genetically-distinct from those of the west coast, differences in the frequency of these haplotypes in the two regions suggest that the individuals from the south coast population are reproductively isolated from those of the west coast (see Chapter 5). In view of this apparent isolation, the possibility that selection pressures have been acting on other loci cannot be discounted. Since the habitat utilised by *A. japonicus* and particularly by fish < 400 mm differs markedly between the west and south coasts, different selection pressures are likely to be influencing their life history characteristics in each of these regions.

Previous studies have explained the utilisation of estuaries by juvenile marine fish with respect to the availability of calm waters, shelter, suitable food and protection from piscivorous predators (Blaber and Blaber, 1980; Kennish, 1986; Cyrus and Blaber, 1987a, 1987b; Blaber, 2000; Paterson and Whitfield, 2000a, 2000b; McLusky and Elliot, 2004). Given the benefits of estuaries, it is thus likely that juvenile *A. japonicus* on the south coast experience lower rates of natural mortality than fish of comparable size on the west coast, *i.e.* where there is a paucity of permanently-open estuaries and the juveniles of many species, including *A. japonicus* (Aylmore and Anderson, 2003; Farmer *et al*, 2005), recruit into low energy nearshore waters (Lenanton, 1982). However, since there have been few studies in Western Australia of the diets of those species that are known elsewhere to prey on the juveniles of nearshore coastal sciaenids, *e.g.* dolphins and sharks (Cliff *et al.*, 1989; Cliff and Dudley, 1991; Ross *et al.*, 1994; de Oliviera Santos *et al.*, 2002; Gannon and Waples, 2004; Barros *et al.*, 2004; Bethea *et al.*, 2004), the extent of this predation cannot be quantified.

Life history theory predicts that reduced adult survival will select for earlier maturation and increased reproductive effort, while reduced juvenile survival will select for the opposite (Law, 1979; Michod, 1979; Kozlowski and Wiegert, 1987). This theory has been supported by laboratory experiments (Rose, 1984; Luckinbill and Clare, 1986,

1987; Reznick *et al*., 1990), as well as comparative data from wild populations (Leggett and Carscadden, 1978; Reznick and Endler, 1982; Stearns, 1983). Changes in the relative mortality rates of different age or size classes can thus lead to an alteration in optimal age and size at maturity. Furthermore, size selective predation over several generations can result in genetically-based differences in the age and size at maturity of prey (Reznick *et al*., 1990; Wellborn, 1994). Thus, the juveniles of *A. japonicus* on the west coast may be experiencing a higher rate of natural mortality through predation, with this selective pressure favouring those individuals that mature later and at a larger size, while the opposite situation would be true for *A. japonicus* on the south coast.

The high energy coastlines and prevalence of permanently-open estuaries in both New South Wales and South Africa, accounts for *A. japonicus* predominantly recruiting into estuaries in those regions. While *A. japonicus* attains maturity at a similarly small size in New South Wales as in the south coast estuarine population examined during the present study, maturity is attained at a much larger size in South Africa (Griffiths, 1996). The larger size at maturity of South African *A. japonicus* may be due to their genetic distinctness from Australian *A. japonicus* (Klopper, 2006; see also Chapter 5), or due to responses to different selection pressures, as the estuaries of that region are likely to differ in terms of their productivity, availability of habitat and abundance of piscivorous predators.

4.4.3 Spawning period

The trends exhibited by the GSIs and the prevalence of stage V/VI gonads indicate that the timing and duration of the spawning period of *A. japonicus* on the west coast of Australia varies greatly. On the lower west coast, the spawning period of *A. japonicus* appears to be related to seasonal water temperatures, with this period coinciding with those months when the mean monthly water temperatures exceed *ca* 19°C, *i.e.* between

November and April (Fig. 4.5). Water temperatures have been linked with spawning activity in a number of teleost species, including sciaenids (*e.g.* Brown-Peterson and Thomas, 1988; Peters and McMichael, 1990; Saucier and Baltz, 1993; Wilson and Nieland, 1994; Connaughton and Taylor, 1995). The highest proportion of fish with stage V/VI gonads were observed from November to February on the lower west coast, which is comparable with the spawning period of *A. japonicus* on the south coast and at similar and higher latitudes throughout southern Australia. For example, Hall (1986) reported that *A. japonicus* spawns between November and January in South Australian waters. In central New South Wales (*ca* 35˚S), spawning of *A. japonicus* appears to take place between November and March (Silberschneider and Gray, 2005), which has been corroborated by the collection of small larvae between February and April (Miskiewicz, 1987; Gray, 1995; Gray and Miskiewicz, 2000), and of small juveniles 20-80 mm in total length between April and June (Anon., 1981).

The trends exhibited by the GSIs and the prevalence of stage V/VI gonads demonstrate that *A. japonicus* spawns throughout much of the year on the upper west coast. This probably reflects the fact that the mean monthly water temperatures for Kalbarri and Carnarvon do not fall below the minimum temperature at which spawning occurs on the lower west coast, *i.e. ca* 19°C, and which apparently limits the spawning period in that region. While the reproductive biology of *A. japonicus* has not been studied at a similar latitude on the east coast of Australia, West and Walford (2000) reported that juvenile *A. japonicus* < 100 mm total length were present throughout the year in two estuaries between *ca* 28˚50'S and 29˚30'S in northern New South Wales. Although the vast majority of comparisons of the timing and duration of spawning of populations of a species at very different latitudes have been conducted in the Northern Hemisphere (*e.g.* Vouglitois *et al*., 1987; Conover, 1992; Barbieri *et al*., 1994; McBride *et al*., 2002; Abookire and Macewicz, 2003), the spawning periods of teleost fishes have

been shown, in general, to commence earlier and last longer in populations at lower latitudes (see Conover, 1992). In his review, Conover (1992) proposed that the spread of spawning over a longer period at lower latitudes is related to the presence of a longer growing season and a shorter winter.

While water temperature is likely to be the main environmental factor influencing the spawning period of *A. japonicus* in South Africa, the spawning of this sciaenid also coincides with peak periods of freshwater discharge from the estuaries of that region (Griffiths, 1996). Griffiths (1996) hypothesised that this strategy enhances the recruitment of early juvenile *A. japonicus* into South African estuaries. However, this is certainly not the case in Western Australia. Although spawning on the upper west coast occurs throughout the year, rainfall is low and sporadic and, as a result, there are also relatively few rivers and thus estuaries throughout that region (Brearley, 2005). Furthermore, on the lower west and south coasts, *A. japonicus* spawns during the driest months of the year and thus some months before there is any consistent substantial rainfall (Sturman and Tapper, 1996; Brearley, 2005).

4.4.4 Spawning mode

As the ovaries of the mature females of *A. japonicus* caught during the spawning period contained previtellogenic, cortical alveolar and yolk granule oocytes, and occasionally hydrated oocytes and/or post-ovulatory follicles, this sciaenid is an indeterminate spawner *sensu* Hunter and Macewicz (1985). Since the potential annual fecundity of *A. japonicus* is therefore not fixed prior to the commencement of the spawning period, any estimate of this variable must take into account both spawning frequency and batch fecundity. Although fecundity has not been determined for any wild populations of *A. japonicus*, such data are available for cultured individuals (Battaglene and Talbot, 1994). The latter workers estimated that fish with a total weight of *ca* 10 kg produce *ca*

1 000 000 eggs. However, it is not known to what extent estimates of fecundity derived from hormone-induced egg production by hatchery-reared fish would be similar to those derived from wild *A. japonicus*. Battaglene (1996) also reported that, in captivity, *A. japonicus* is a group synchronous spawner. Although sciaenids have a relatively high fecundity, which would be of value when their stocks are heavily exploited (Musick, 1999; Powles *et al.*, 2000), some members of this family are particularly vulnerable to fishing (*e.g.* Cisneros-Mata *et al.*, 1995; Sadovy and Cheung, 2003; see also Chapter 1).

4.4.5 Spawning locations

Large numbers of preflexion larval *A. japonicus* were collected in plankton trawls conducted in late spring/early summer in nearshore marine waters, *i.e.* 5-22 m depth, at a latitude of *ca* 32°S on the lower west coast between 2001 and 2005 (C. Wakefield, Murdoch University, unpubl. data). Since *A. japonicus* eggs and larvae have not been recorded during extensive plankton trawling conducted farther offshore (Muhling, 2006), spawning appears to be confined to the nearshore zone. In New South Wales, early preflexion larvae have also been collected near the substratum in depths of *ca* 30 m in the coastal waters of New South Wales (Gray, 1995), while plankton trawling in the coastal embayment of Botany Bay has also resulted in the capture of numerous early larval *A. japonicus* (Steffe, 1991). Thus, as has been documented for South African *A. japonicus* (Griffiths, 1996), this sciaenid also appears to spawn in the nearshore coastal waters of Australia.

The lower reaches of the Swan River Estuary, *i.e.* Mosman Bay, was identified during the present study as a spawning ground for *A. japonicus* on the lower west coast for the following reasons; 1) *A. japonicus* was only caught in Mosman Bay during the spawning period, *i.e.* November to April, with the restriction of their presence to these months being verified independently by the use of acoustic methods (Parsons *et al.*,

2006), 2) All of the *A. japonicus* caught in Mosman Bay had total lengths > L_{50} at first maturity, 3) Several of the females caught in this same region had stage VI ovaries, *i.e.* containing hydrated oocytes and/or post-ovulatory follicles, which indicates those individuals were about to spawn or had recently spawned.

As the lower reaches of the Swan River Estuary is essentially a marine environment during the spring and summer months (Stephens and Imberger, 1997), it is proposed that Mosman Bay provides environmental conditions analogous to those in the coastal waters in which this species typically spawns (see Silberschneider and Gray, 2007). Although this is the first confirmed case of estuarine spawning by *A. japonicus*, fish with stage V gonads were caught in Oyster Harbour on the south coast during the present study and approximately half of the mature males and one third of the mature females came from estuarine catches during the study of Silberschneider and Gray (2005) in New South Wales.

Although few species typically spawn within estuaries in most other regions of the world (Haedrich, 1983; Dando, 1984), several species complete their life cycle in the estuaries of south-western Australia (Potter and Hyndes, 1999). Estuarine spawning has also been reported for several other members of the Sciaenidae and is particularly common amongst sciaenids found in the vicinity of the Río de la Plata Estuary, which is located between Argentina and Uruguay. *Micropogonias furnieri* (Macchi *et al*., 1996, 2003; Acha *et al.*, 1999), *Pogonias cromis* (Macchi *et al.*, 2002), *Macrodon ancylodon* (Millitelli and Macchi, 2000), *Paralonchurus brasiliensis* (Berasategui *et al.*, 2004) and *Cynoscion guatucupa* (Berasategui *et al.*, 2004) all spawn in that system at various times. However, several of the estuarine spawning species in the Río de la Plata Estuary, including *Micropogonias furnieri*, *Macrodon ancylodon* and *Paralonchurus brasiliensis*, spawn in marine waters in the Patos Lagoon region of Brazil (Sinque and Muelbert, 1997).

4.4.6 Diel periodicity of spawning in the Swan River Estuary

All of the female *A. japonicus* caught in the lower reaches of the Swan River Estuary and which had ovaries containing hydrated oocytes and newly-formed POFs were caught between 21:00 and 23:30 h. Since Parsons *et al.* (2006) also concluded that the vocal activity of *A. japonicus* in Mosman Bay occurred only in the evening, with a peak *ca* one hour after sunset (Parsons *et al.*, in prep.), this species appears to spawn at night in Western Australian waters. South African *A. japonicus* also spawns at night (Griffiths, 1996), while nocturnal spawning has been commonly reported amongst sciaenids (*e.g.* Holt *et al.*, 1985; Saucier and Baltz, 1993; Connaughton and Taylor, 1995; Macchi *et al.*, 2003; Bialetzki *et al.*, 2004; Yamaguchi *et al.*, 2006), which also supports the theory that the diel time of spawning is often uniform within a taxonomic family (Ferraro, 1980). Since many sciaenids use sound to locate mates during the spawning season (Holt *et al.*, 1985), they do not depend on light for their courtship behaviour. The nocturnal spawning of *A. japonicus* in Western Australia may have a number of advantages. As zooplanktivores are mainly visual feeders and these predators are particularly abundant in estuaries (Johnson *et al.*, 1990; Morgan, 1990), a nocturnal spawning regime may reduce the effects of predation and increase survivorship of eggs and larvae (Holt *et al.*, 1985). Since sunlight can also have a deleterious effect on pelagic eggs in particular, spawning during darkness may further enhance egg survival (Saucier and Baltz, 1993).

All of the female fish with ovaries containing hydrated oocytes were also caught immediately prior to the peak of high tide in the lower reaches of the Swan River Estuary and it is thus likely that the fertilised eggs are transported downstream and out of the system on the ebb tide. *Rhabdosargus sarba* also spawns at night during ebb tides in the summer months in the lower reaches of the Swan River Estuary (Hesp *et al.*, 2004b). Thus, while the eggs/larvae of *A. japonicus* were absent during extensive

sampling of the ichthyoplankton of the lower reaches of the Swan River Estuary (Gaughan *et al.*, 1990), the absence of any *R. sarba* eggs/larvae in these samples suggests that trawling was conducted outside the times when these species spawn in this system. Since planktivorous fishes, such as *Spratelloides robustus*, are particularly abundant in the lower reaches of the Swan River Estuary (Hesp *et al.*, 2004b), a rapid movement of the eggs of both of these species out of the estuary would greatly enhance their chances of survival.

5.0 Population genetic structure

5.1 Introduction

5.1.1 Stock identification and the genetic approach

While the term stock has been variously applied, it is often used by fisheries managers to describe a group of fish exploited in a specific area or by a specific method, *i.e.* the fishery stock (Smith *et al*., 1990). Although this definition is useful for the collection of catch and effort data and the application of management strategies, it does not represent the true substructuring of fish species and is thus unlikely to be the most appropriate unit for management (Carvalho and Hauser, 1994). Various biological stock definitions have been put forward in an attempt to overcome this problem, but the definition proposed by Ihssen *et al*. (1981), namely that "a stock is an intraspecific group of randomly mating individuals with temporal and spatial integrity" is still the most widely accepted. The biological stock concept recognises that species are rarely panmictic over their entire range, but instead are composed of a series of subpopulations that are at least partially reproductively isolated from one another (Shaklee and Currens, 2003). Coupled with such partial reproductive isolation, the typically restricted distributions of subpopulations of fish in time and space provide the basis for local adaptation via selection, which can result in stocks that are effectively independent in terms of their life history characteristics and thus also in their response to harvesting and exploitation (Carvalho and Hauser, 1994). Identifying such subpopulations is essential from a fisheries management perspective, as these different stocks are likely to require management plans that are based on their own unique set of life history characteristics.

Various methods have been used to examine the stock structures of teleost species, all of which focus, either directly or indirectly, on discerning the patterns of dispersal of those species. Some of the more commonly used methods include the examination of data on the distribution and abundance of various life history stages, the use of natural or artificial marks and tags, meristics and morphometrics, the examination

of calcified structures, the study of life history parameters and molecular techniques (see Pawson and Jennings, 1996; Jennings *et al*., 2001). Over the past 10 to 15 years, however, fisheries scientists have increasingly used molecular techniques for stock discrimination, while fisheries managers have become increasingly concerned with identifying and assessing the genetic risks associated with various actions and inactions (Shaklee and Currens, 2003). The increased popularity of molecular methods is due largely to their ability to rapidly yield valuable information on the population structure of a species and to cost less than other methods, *e.g.* tagging experiments (Shaklee and Currens, 2003). In addition, molecular markers can provide information about the population of origin of individuals, which is an essential component of stock discrimination, whereas other methods typically overlook factors, such as dispersal during the early phases of the life-history, that may be critical in this regard (Pawson and Jennings, 1996).

While molecular markers have become the standard tool for the assessment of stock structure (Johnson, 2000), they have a number of disadvantages that need to be taken into account. For example, determining whether two samples are from a single panmictic population or from two separate stocks is not always straight forward using molecular techniques, particularly if no genetic differences are detected. This is because the absence of significant genetic differentiation indicates either that (1) the samples constitute a single stock or (2) there are two stocks, which could not be resolved by the test that was used (Ward, 2000). Thus, while the null hypothesis of panmixia can be rejected if heterogeneity is detected, a failure to reject the null hypothesis does not mean the null hypothesis is true (Ward, 2000). Clearly, a finding of sample heterogeneity allows for more powerful conclusions regarding stock structure than a finding of sample homogeneity.

A number of genetic markers have been used to identify subpopulations or stocks of teleost species, with these commonly including allozymes (*e.g.* Phelps *et al*., 1994; Chaplin *et al*., 1998), mitochondrial DNA (*e.g.* Aboim *et al*., 2005; Froukh and Kochzius, 2007) and nuclear-encoded microsatellites (*e.g.* Gold and Turner, 2002; Knutsen *et al*., 2003). Each of these genetic methods has their own unique set of advantages and disadvantages, which have been extensively reviewed in the context of stock assessment (see Carvalho and Hauser, 1994; Ward and Grewe, 1994; Shaklee and Currens, 2003). It should also be recognised that no single genetic marker is universally superior for all species and situations. Indeed, as the above molecular markers are characterised by differences in mutational properties, modes of inheritance and effective population sizes (*e.g.* Beheregaray and Sunnucks, 2001; Apte and Gardner, 2002; Bilodeau *et al*., 2005), it is a combination of these markers that often provides the most adequate overview of stock structure. Nevertheless, the choice of marker(s) often depends on the outcome of a balance between the time and financial cost of generating the data and the quality and quantity of the information required. Investigations of the stock structure of teleost species commonly employ nucleotide sequence information from the control region of the mitochondrial DNA because this type of marker typically provides a rapid, cost-effective and reliable method of generating relatively high resolution genetic data (Avise, 1994). However, since the mtDNA molecule is maternally inherited in its entirety, this marker suffers from providing only a single-locus estimate of female gene flow (Hutchinson *et al*., 1974; Avise and Vrijenhoek, 1987; May and Grewe, 1993).

5.1.2 *Argyrosomus japonicus*, dispersal potential and results of previous research

Much of the life history and environmental information that is required to understand the dispersal potential of *A. japonicus* in Western Australian waters, *e.g.* such as the

coastal topography, oceanography, typical spawning locations, movements and the utilisation of habitat by juveniles and adults, has been provided in Chapters 2-4. What is lacking, however, is a description of the early life history characteristics of this sciaenid. The eggs of *A. japonicus* are pelagic, *ca* 938 μm in diameter and, in water temperatures of 23°C in the laboratory, hatch between 28 and 30 hours after spawning (Battaglene and Talbot, 1994). Upon hatching, the larvae have lengths of 2.2-2.3 mm and, in captivity, remain pelagic for *ca* 12 days (Battaglene and Talbot, 1994; Clark *et al*., 2005). Notochord flexion occurs at a length of *ca* 5 mm, after which the larvae are capable of swimming in inertial environments, and settlement occurs at lengths of 12-13 mm and *ca* one month old (Clark *et al*., 2005). Plankton sampling in New South Wales has demonstrated that the pre-flexion larval *A. japonicus* predominantly occupy subsurface waters (Steffe, 1991; Gray, 2005), which suggests that even the early larval stages may prefer the deeper parts of the water column where they may be less affected by the prevailing currents.

Additional information on the dispersal potential of the juveniles and adults of *A. japonicus* is available from tag-recapture studies, which have been carried out in New South Wales (Thomson, 1959; West, 1993, Silberschneider and Gray, 2005; Taylor *et al*., 2006), South Australia (Hall, 1984) and Western Australia (Farmer, 2003). These studies have consistently demonstrated that juvenile fish can remain for extended periods in particular areas, such as in the estuaries of New South Wales and South Australia and in certain nearshore coastal waters in Western Australia, and that adult *A. japonicus* are capable of migrating relatively large distances along the coast. For example, the maximum distance covered by a recaptured adult fish in each of these states is between 200 and 400 km. The available data thus suggest that *A. japonicus* has the potential to disperse over hundreds of kilometres in Australian waters. However,

there are further factors that might confound this potential and the extent to which it is realised is largely unknown.

Marine teleosts generally produce a large number of eggs and larvae that are potentially capable of being dispersed over vast distances via passive or active mechanisms, and since there are few absolute barriers to gene flow in the marine environment, they are traditionally expected to show minimal genetic subdivision in marine ecosystems (Gyllensten, 1985; Palumbi, 1992, 1994; Ward *et al*., 1994). While genetic differences between populations of marine teleosts are often small and occur over large geographical distances (Palumbi, 1994), substantial genetic divergence has been recorded among some populations over relatively small spatial scales (*e.g.* Planes *et al*., 1996, 1998; Santos *et al*., 2006). In these instances, genetic differentiation may arise among populations of marine teleosts due to behavioural factors, such as natal site homing (*e.g.* Planes *et al*., 1996, 1998; Gold *et al*., 1999), or the presence of small-scale physical barriers, *e.g.* ocean currents and relatively discrete water bodies such as estuaries and sheltered embayments (Ayvazian *et al*., 1994; Johnson *et al*., 1994; Swearer *et al*., 1999).

It is well recognised that estuaries and sheltered embayments are important nursery areas for many marine teleosts (Potter *et al*., 1986; 1990), including numerous sciaenids (*e.g.* Cowan Jr. and Birdsong, 1985; Griffiths, 1996; Rooker *et al*., 1998; Rowell *et al*., 2005). However, due to their physical isolation from oceanic currents and the high variability of their environmental conditions, these systems may also offer special opportunities to certain marine teleosts for local isolation and genetic divergence (see Watts and Johnson, 2004). Thus, although *A. japonicus* has a high potential for dispersal, this may not be always realised, especially in locations where they utilise estuaries and large marine embayments.

Information on the population structure of *Argyrosomus japonicus* is scarce throughout the extensive, but fragmented, worldwide distribution of this species. The most comprehensive data set is that recorded for this species in South African waters. Data obtained from mtDNA control region sequences indicate, in particular, that the adults of *A. japonicus* on the eastern coast of South Africa comprise several geographically-separated spawning populations rather than a single interbreeding unit (Klopper, 2005). The presence of spawning aggregations, which are discrete in space and time in the coastal waters of KwaZulu/Natal between August and November and off the southern and south-eastern Cape regions between October and January (Griffiths, 1996), lends further credence to Klopper's (2005) multiple-stock hypothesis. Regional differences in otolith morphology and particularly in the relationship between otolith dimension and total length have also been determined for South African *A. japonicus* (Griffiths and Hecht, 1995a). However, since otolith morphology is primarily influenced by environmental conditions (Campana and Casselman, 1993), these may not reflect genetic/real population differences. Nevertheless, significant differences in the morphology of the otoliths of different assemblages suggest South African *A. japonicus* is represented by three or more stocks, at least for a substantial portion of their lives (Griffiths and Hecht, 1995a). Thus, the data for South African *A. japonicus* indicate that, despite this species having an apparently high potential for dispersal, population differentiation occurs over regional scales, at least in some locations.

Information on the population structure of *A. japonicus* in Australian waters is limited to the genetic analysis conducted by Black and Dixon (1992). These authors used allozyme electrophoresis and direct sequencing of the cytochrome b region of mtDNA to examine broadly the population structuring of *A. japonicus* in New South Wales, South Australia and Western Australia. Their attempts to sequence the cytochrome b region of mtDNA for *A. japonicus* from Western Australia proved

unsuccessful and this region varied only slightly between New South Wales and South Australian populations. Yet, data from allozyme electrophoresis suggest that a separate sub-population of *A. japonicus* exists in Western Australia, with the possibility of further sub-structuring between the populations in New South Wales and South Australia (Black and Dixon, 1992). Since this study included only a small number of samples from two locations in Western Australia, *i.e.* Carnarvon/Shark Bay and Mandurah, it did not yield definitive information regarding the population genetic structure of *A. japonicus* throughout that state.

5.1.3 Aims

The above information demonstrates that the population structure of *A. japonicus* in Western Australia needs to be investigated. In particular, it is likely to be a useful step in helping to understand the basis for the biological differences between the populations sampled on the west coast and in Oyster Harbour on the south coast (see Chapters 3 and 4). Despite similarities in biology on the west coast, it is also of particular relevance to know if there are multiple stocks along that coast as, for example, it will determine the spatial scale at which the fisheries for this species should be managed and the potential for any stocks to diverge in the future. Thus, the overall objective of this chapter was to use a mitochondrial DNA marker to investigate the population genetic structure of *A. japonicus* in Western Australia focussing, in particular, on the assemblages in those sites for which the biological data were obtained. The specific aims were to (1) investigate whether multiple stocks are present among the biologically-similar assemblages on the west coast and (2) compare the unusual population in Oyster Harbour on the south coast with those on the west coast. In addition, a limited amount of sequence data was also included for *A. japonicus* from New South Wales and South Africa to place in context the results obtained for Western Australian individuals.

5.2 Materials and methods

5.2.1 Collection of sample tissue

The *A. japonicus* used for analysing genetic variation within and between assemblages in Western Australia were collected from the main locations sampled to obtain biological data (see Chapter 2), namely Carnarvon, Geraldton and Perth on the west coast and Oyster Harbour on the south coast (Table 5.1; Fig. 5.1). Individuals from the last locality were caught exclusively using composite sunken gill nets, while all others were predominantly caught using rod and line. Gill net specifications and the setting regime are provided in Chapter 2, along with a description of the rigs used when rod and line angling. Roughly 3 g of muscle tissue was dissected from the shoulder area of each fish, *i.e.* above the lateral line immediately behind the head, and then placed in a cryovial and stored at -80°C. Bita Archangi of Queensland University of Technology provided pectoral fin tissue for New South Wales *A. japonicus*, which had been collected from the lower reaches of the Hawkesbury River (Table 5.1; Fig. 5.1).

Table 5.1. Details of all Australian samples used in genetic analyses. WA = Western Australia, NSW = New South Wales, BF or SH/MU = Bryn Farmer or Steeg Hoeksema/Murdoch University, BA/QUT = Bita Archangi/Queensland University of Technology, *n* = sample size.

Region	Sample	Sample code	Date collected	Latitude	Longitude	Collector	*n*
WA west coast	Carnarvon	C	11/2004	24°53´S	113°39´E	BF/MU	30
	Geraldton	G	6/2003-11/2004	28°47´S	114°37´E	BF/MU	38
	Perth	P	4/2004-4/2006	31°57´S	115°51´E	BF/MU	34
WA south coast	Oyster Harbour	O	2/2006-2/2007	35°01´S	117°53´E	SH/MU	30
NSW	Hawkesbury River	H	2/2004-4/2004	33°37´S	151°18´E	BA/QUT	5

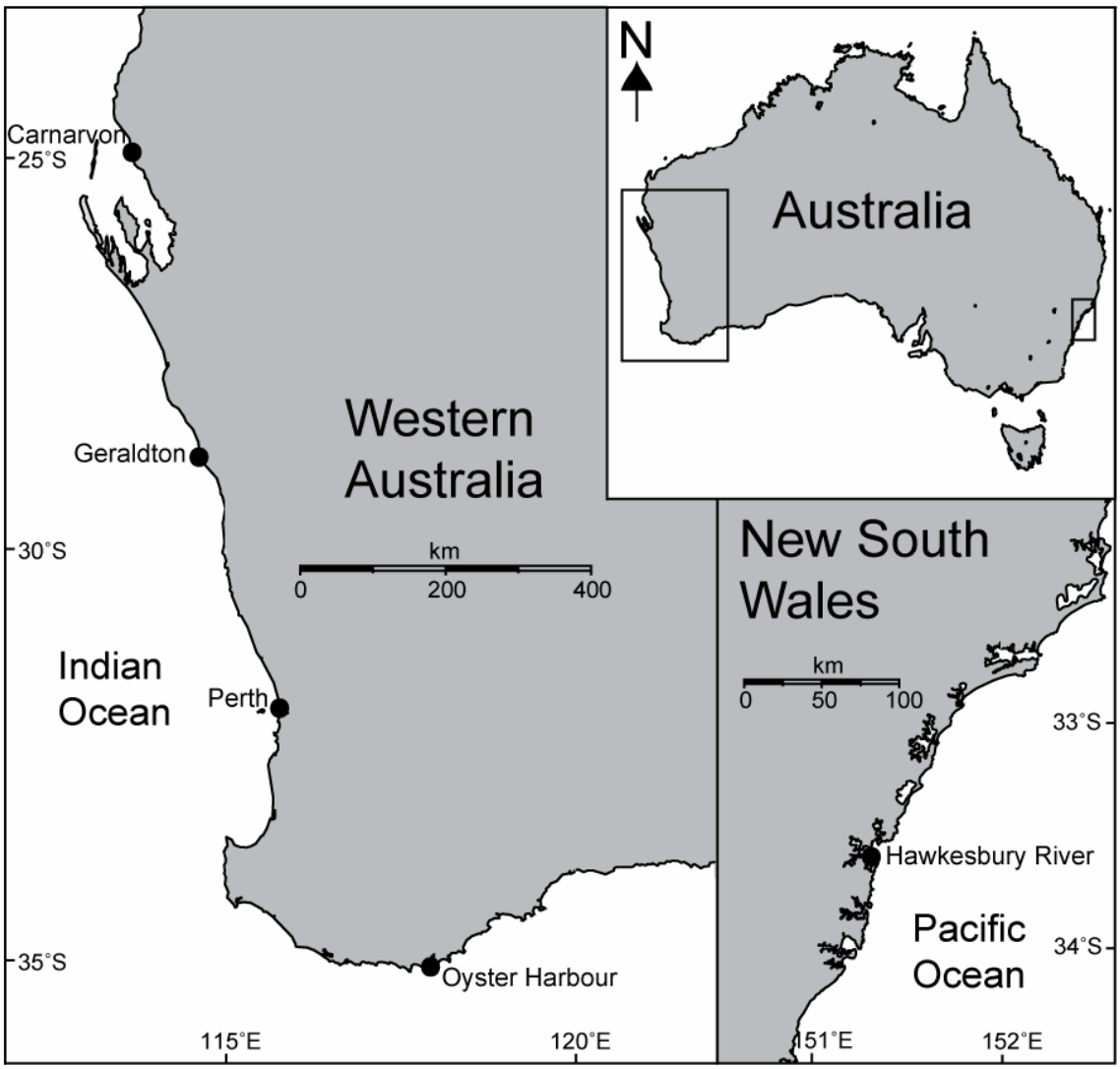


Figure 5.1. Map showing the locations in Western Australia and New South Wales from which the *Argyrosomus japonicus* used in genetic analyses were sampled.

5.2.2 DNA extraction

Total genomic DNA was extracted from the muscle and pectoral fin tissue samples using the MasterPure^{TM} DNA Purification Kit (Epicentre Technologies). However, in the case of the "tougher" fin tissue, the following slight modification was made to the manufacturer's protocol - 2 µL of Proteinase K (50 µg/ µL) was added to each tube containing 300 µL of Tissue and Cell Lysis Solution and the period of incubation at 65°C was increased to 1 h. The quality of DNA extraction from both types of tissue was verified by subjecting a 10 µL aliquot, containing 2 µL of the DNA preparation, 2 µL of

dense dye and 6 µL of double-deionised H_2O, to electrophoresis in a 2% agarose gel. The gel was then stained with ethidium bromide and viewed under ultraviolet light using a Gel Doc 2000 and the computer-imaging program Quantity One (version 4.1.0; Bio-Rad, 1998). The concentration of extracted DNA was compared to that of a lambda standard and successful DNA preparations were stored at -4°C.

5.2.3 PCR amplifications

Polymerase chain reaction (PCR) was used to amplify a 352 bp portion of the 3' end of the mtDNA control region of all *Argyrosomus japonicus*. The control region was targeted for analysis because in most vertebrates it has the following characteristics. It consists of a central conserved region, which facilitates the development of suitable primers, and this is surrounded by two adenine-rich and highly variable end domains that are characterised by substitution rates five- to 10-fold higher than any other portion of the mtDNA molecule and are thus likely to reveal relatively high levels of intraspecific variation (Brown, 1983; Moritz *et al.*, 1987; Kocher *et al.*, 1989). 'Universal primers' (Kocher *et al.*, 1989) failed to amplify the control region of *A. japonicus* in the present study, which is consistent with the findings of Black and Dixon (1992) for Australian *A. japonicus*. Arrie Klopper (University of Pretoria) kindly provided information on a further set of primers that he used to study the population genetic structure of South African *A. japonicus* (Klopper, 2005), but these also failed to consistently amplify the control region for the Australian samples. Thus, forward and reverse primers had to be specifically designed. The forward and reverse primers were based on conserved regions in a multiple alignment of sequences of the whole control region of Australian and South African *A. japonicus*, which was again provided by Arrie Klopper (University of Pretoria). Several potential sets of forward and reverse primers were designed, all of which were analysed for the presence of secondary

structures, *i.e.* hairpins, self-dimers, and cross-dimers, as well as compatible melting temperatures in the primer pairs, using the program NetPrimer (available at http://www.premierbiosoft.com/netprimer/). Based on these criteria, the following primers were selected for use in the forward and reverse reactions, respectively;

ArgCR01-FWD: 5´ TTC CTG GCA TTT GGT TCC TAC 3´

ArgCR01-RVS: 5´ GTT AAT GAT CTC AGG AGT GCT 3´

Each PCR reaction mixture contained *ca* 10 ng of DNA template, 20 µM of each primer, 10 µL of *Taq* buffer (Roche), 0.1mM of each of the dNTPs (Promega) and 0.1 µL of *Taq* polymerase (Roche), and was adjusted to a final volume of 50 µL with PCR grade water. Amplification of the target region was carried out using a step-up PCR profile, characterised by an initial denaturation phase at 94°C for 5 min, followed by 25 amplification cycles, with each cycle consisting of 30 sec of denaturation at 94°C, 30 sec of annealing at 62°C and 30 sec of extension at 72°C, followed by a final 5 min of extension at 72°C. The success of PCR amplification was assessed by subjecting a 10 µL aliquot of each reaction mixture to electrophoresis in a 2% agarose gel. The gel was then stained with ethidium bromide and viewed under ultraviolet light using a Gel Doc 2000 and BioRad Quantity One software (version 4.1.0). The concentration of the DNA fragment in the reaction mixture was estimated using a PhiX174/HaeIII marker (Promega). The products of the PCR reaction were then cleaned for sequencing using Qiaquick spin columns (Qiagen), according to the manufacturer's protocol.

5.2.4 Mitochondrial DNA sequencing

Sequencing was carried out using the dye terminator cycle sequencing method. Each sequencing reaction was prepared using *ca* 30 ng of cleaned PCR product, 3.2 pmol of

the forward or reverse primer and a Big Dye 3.1 terminator cycle sequencing ready reaction kit (Applied Biosystems Inc.). The products of sequencing were electrophoresed and the raw chromatograms generated using an Applied Biosystems 3230 DNA Analyzer automated sequencer.

5.2.5 Sequence preparation and alignment

Raw chromatogram data were edited using GeneTool™ Lite (version 1.0; Wishart *et al*., 2000). The forward and reverse sequences generated for each individual were aligned and the primer sequences removed from either end. For each individual, the forward and reverse sequences were compared and any alignment errors or base misreads were corrected and, ultimately, a forward-reading consensus sequence was generated. The identity, location and orientation of preliminary sequences were confirmed by BLAST searches of the GenBank database (http://www.ncbi.nlm.nih.gov/blast/). A multiple alignment of the forward consensus sequences of all individuals was performed with GeneTool™ Lite (version 1.0; Wishart *et al*., 2000), and those nucleotide substitutions that were found in only one individual were compared to the raw chromatogram data for verification. Each unique nucleotide sequence was allocated haplotype status and named according to the geographic source and a number.

5.2.6 Data analyses

Once all sequence data had been generated and aligned, it became apparent that numerous indels, *i.e.* insertion or deletion substitutions, were present. Since recent studies indicate that indels potentially yield information about the distribution of genetic variation (Pearce, 2006), software for all subsequent data analyses was selected so that the data for these sites could be taken into account. The number of haplotypes, location

of polymorphic sites and base compositions for all nucleotide positions of Australian haplotypes were derived using the program DnaSP (Rozas *et al.*, 2003).

Interpretation of the population genetic structure of *A. japonicus* in Australia is influenced by whether the patterns of variation shown by the control region conform to those expected for a neutral marker in mutation-drift equilibrium (see Ford, 2002). Furthermore, as the mtDNA of a variety of organisms have been shown to deviate from a strictly neutral model of evolution (*e.g.* Nachman, 1998; Rand and Kann, 1998; Rand, 2001), it is not safe to assume *a priori* that mtDNA evolves as a strictly neutral marker (Ballard and Whitlock, 2004). There is a wide range of tests that can be used to assess the neutrality of mtDNA sequence information. Since no single test provides a definitive test of neutrality or departures from equilibrium, with each measuring a slightly different aspect of a given data set, the use of multiple such tests can yield more information about a data set than any single test. Thus, the selective neutrality of the mtDNA control region fragment amplified in the present study was examined using a range of the more commonly applied neutrality tests, namely Tajima's (1989) test, Fu's (1997) F_S-test and Fu and Li's (1993) tests. Tajima's (1989) test and Fu's (1997) F_S-test were conducted using Arlequin (version 3, see Excoffier *et al.*, 2005), while Fu and Li's (1993) tests were conducted using DnaSP (see Rozas *et al.*, 2003). For the neutrality tests described above and for all subsequent multiple tests, a sequential Bonferroni procedure was applied to assess the statistical significance of the probability values (Rice, 1989).

The level of diversity in the mtDNA control region of each of the Australian samples and among all of the Australian samples combined was expressed in terms of haplotype diversity (h) and nucleotide diversity (π). Haplotype diversity is the probability that two randomly-selected individuals exhibit the same haplotype, while nucleotide diversity is the average proportion of nucleotide differences between all pairs

of sequences in the sample (Nei, 1987). Point estimates of these two diversity indices and the associated standard errors were calculated using Arlequin (version 3.1.1; Excoffier *et al*., 2005). Tamura and Nei's (1993) substitution model was selected for the calculation of nucleotide diversity due to its applicability to the highly variable control region. A gamma correction, which was determined using the maximum likelihood method in TREE-PUZZLE (Schmidt *et al*., 2002), was incorporated into the calculation of nucleotide diversity.

Analysis of molecular variance (AMOVA; Excoffier *et al*., 1992) was used to assess how the genetic variation was partitioned within and among the Australian samples of *A. japonicus* using Arlequin (version 3.0; see Excoffier *et al*., 2005). Significance tests at these hierarchical levels, *i.e.* within and among Australian samples, were performed using, with 10 000 permutations, the nonparametric permutation approach described by Excoffier *et al*. (1992).

Exact probability tests were used to determine the statistical significance of any differences in the frequencies of haplotypes between all pairs of Australian samples. The associated null hypothesis was that the haplotype frequency distributions in the two samples being compared were not significantly different. Probability values were estimated using the Markov chain method with 10 000 steps (see Raymond and Rousset, 1995), as implemented in Arlequin (version 3, Excoffier *et al*., 2005). Exact probability tests were employed as they are not biased by small sample sizes or low haplotype frequencies (Raymond and Rousset, 1995).

The extent of haplotype frequency variation among the Australian samples was also examined using *F*-statistics (Weir and Cockerman, 1984). The raw values of F_{ST} were calculated over all samples and between all pairs of samples using FSTAT (version 2.9.3.2, available at http://www2.unil.ch/popgen/softwares/fstat.htm, Goudet, 1996). In order to minimise the bias in F_{ST} estimates introduced by variation in the

amount of underlying genetic polymorphism between samples, these raw values of F_{ST} were standardised (see Meirmans, 2006). Standardisation of these raw values was achieved by dividing them by the maximum possible value of F_{ST}, which was calculated by recoding the data such that no alleles are shared between samples (Meirmans, 2006). Maximum values of F_{ST} were also calculated using FSTAT (version 2.9.3.2, Goudet, 1996), while raw F_{ST} values were recoded using RecodeData (version 0.1, available at http://www.bentleydrummer.nl/software/software/Other%20software.html). The null hypothesis that the value of the index did not differ significantly from zero, *i.e.* no genetic differentiation, was tested using 10 000 permutations in FSTAT (version 2.9.3.2, Goudet, 1996). In order to resolve the spatial patterns of population differentiation, multi-dimensional scaling (MDS; Hair *et al*., 1992) ordination was used to map the standardised values of F_{ST} between each pair of samples in two-dimensional space. This ordination technique has an advantage over cluster analyses as it does not force samples into discrete clusters when genetic variation is continuous (Lessa, 1990; Clarke, 1993). All MDS ordinations were carried out employing PRIMER (version 6; Clarke and Warwick, 2001).

The evolutionary relationships among all control region haplotypes was investigated by constructing a haplotype network based on the parsimony method of Templeton *et al*. (1992) using TCS version 1.13 (Clement *et al*. 2000). This investigation included the haplotypes from both Western Australia and New South Wales, as well as five haplotypes from South Africa kindly provided by Arrie Klopper (University of Pretoria). The sequence data for South African *A. japonicus* comprised five haplotypes that were among the most divergent identified during the study of Klopper (2005), which included samples obtained from nearshore waters between St Lucia Estuary (28°00´S, 32°40´E) and De Hoop (34°35´S, 20°21´E). However, since the sequence data provided for South African individuals included the entire mtDNA

control region, these had first to be cropped to include the same portion that was amplified for the Australian specimens. For TCS analysis, the maximum number of substitutions required to connect any two haplotypes parsimoniously, *i.e.* with 95% confidence, was estimated and the network built in a stepwise manner by firstly linking sequences with the smaller number of differences.

The level of sequence divergence between the Australian and South African samples was further investigated using the Kimura two parameter (K2P) distance model (Kimura, 1980).

5.3 Results

5.3.1 Overall nucleotide compositions and levels of polymorphism

A 352 bp portion of the 3' end of the mtDNA control region was sequenced for each of 131 individuals of *A. japonicus* from the four locations sampled in Western Australia. The average base composition of this portion of mtDNA for all Western Australian individuals combined was; A, 27.7%; T, 30.5%; C, 23.8%; G, 18.0%, with a clear bias towards adenine and thymine, *i.e.* 58.2%. Biases towards adenine and thymine in the mtDNA of teleosts have been commonly reported (*e.g.* Meyer *et al.*, 1990; McMillan and Palumbi, 1997; Garber *et al*., 2004; Aboim *et al*., 2005; Frouk and Kochzius, 2007), including for other sciaenids (Seyoum *et al*., 2000).

A comparison between sequences from the four Western Australian locations revealed substitutions at 26 of the 352 sites (Table 5.2). Transitional substitutions comprised the majority of variation amongst haplotypes, *i.e.* 18 sites, while the remainder of the variation was due to transversional substitutions and indels. Since indels were more than twice as prevalent as transversional substitutions, *i.e.* 8 *vs* 3, they were considered an important component of the total variation. The 26 variable positions within this portion of the control region revealed a total of 20 different haplotypes (Table 5.3). The overall haplotype and nucleotide diversities for the Western Australian samples were 0.805 ± 0.03 and 0.017 ± 0.009, respectively.

While the New South Wales sample comprised only five individuals, the average base composition and thus bias towards adenine and thymine were almost identical to those for the Western Australian samples. Furthermore, when the New South Wales sample was included in a pooled Australian sample, the values for overall haplotype and nucleotide diversity remained essentially unchanged. However, it should be noted that among these five individuals were three haplotypes, none of which was present in the Western Australian samples (Tables 5.2, 5.3).

Table 5.2. Location and distribution of the 26 polymorphic sites that define the 20 haplotypes in samples of *Argyrosomus japonicus* from four locations in Western Australia (WA). The three haplotypes (and two additional polymorphic sites) in the limited sample from New South Wales (NSW) are also shown. The positions of each of the polymorphic sites from the start of the control region fragment are indicated in the top row. Dots represent matches with nucleotides present in haplotype 1. Abbreviations for regions are as given in Table 5.1. IND = insertion or deletion substitution. Note that the distribution and abundance of these haplotypes among sampling locations is

		Polymorphic sites																														
		15	20	24	32	74	75	110	138	166	168	169	204	208	214	222	224	231	247	250	256	257	260	261	309	316	333	343	352
Region	**Haplotype**																												
WA	1	T	T	C	A	A	C	A	C	A	G	A	C	A	IND	IND	G	A	A	G	A	A	A	G	A	IND	IND	C	IND
	2	·	G	T	·	·	·	·	·	G	A	·	·	·	A	·	A	·	·	·	G	·	·	A	T	·	T	·	C
	3	·	G	T	·	·	·	·	·	·	A	·	·	·	A	·	A	·	·	·	G	·	·	A	T	·	T	·	C
	4	·	A	·	·	·	T	G	·	·	·	·	·	·	A	·	·	·	G	·	·	·	·	A	·	·	·	·	·
	5	·	A	·	·	·	·	G	·	·	·	G	T	·	A	·	A	·	·	·	·	G	·	A	T	·	·	·	C
	6	C	A	·	·	·	·	·	·	·	·	·	·	G	A	·	A	·	·	·	·	·	·	A	T	·	·	·	·
	7	C	A	·	·	·	·	·	·	·	·	·	·	G	A	·	·	·	·	·	G	·	·	A	T	·	·	·	·
	8	·	A	·	·	·	·	·	·	·	·	·	·	G	A	·	A	·	·	·	·	·	·	A	IND	·	·	·	·
	9	·	A	T	·	·	·	·	·	·	A	·	·	·	A	·	A	·	·	·	G	·	·	A	T	·	T	·	C
	10	·	A	·	·	·	T	G	·	·	·	·	·	·	A	·	A	·	G	·	·	·	·	A	·	C	·	·	·
	11	·	A	·	·	·	T	G	·	·	·	·	·	·	A	G	IND	·	G	·	·	·	·	A	·	·	·	·	·
	12	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	C
	13	·	A	·	C	·	T	G	·	·	·	·	·	·	A	·	·	·	G	·	·	·	·	A	·	·	·	·	·
	14	C	A	·	·	G	·	·	·	·	·	·	·	G	A	·	·	·	·	·	·	·	·	A	T	·	·	IND	·
	15	·	A	·	·	·	T	G	·	·	·	·	·	·	A	·	A	·	G	·	·	·	·	A	·	·	·	·	·
	16	C	A	·	·	G	·	·	·	·	·	·	·	G	A	·	·	G	·	·	·	·	·	A	T	·	·	IND	·
	17	C	A	·	·	·	·	·	·	·	·	·	·	G	A	·	·	·	·	·	·	·	·	A	T	·	·	·	·
	18	·	A	·	·	·	·	G	·	·	·	·	·	·	A	·	A	·	G	·	·	·	·	A	·	·	·	·	·
	19	C	A	·	·	G	·	·	·	·	·	·	T	G	A	·	·	·	·	·	·	·	G	A	T	·	·	IND	·
	20	·	A	·	·	·	T	G	·	·	·	·	·	·	A	·	·	·	G	·	·	·	·	A	·	·	·	IND	·
NSW	21	·	A	·	·	·	·	G	·	·	·	·	T	·	A	·	A	·	·	·	·	G	·	A	T	·	·	·	C
	22	·	A	·	·	·	·	·	·	·	·	G	T	·	A	G	IND	·	·	·	·	G	·	A	T	·	·	·	C
	23	·	A	·	·	·	·	·	T	·	·	G	·	·	A	·	·	·	·	A	·	·	·	A	T	·	·	·	C

Table 5.3. Distribution and abundance of the 20 haplotypes among the four samples of *Argyrosomus japonicus* from Western Australia. The abundance of the three haplotypes in the limited sample from New South Wales is also shown. Abbreviations for regions and sample locations are as given in Table 5.1. n = sample size, n_H = number of haplotypes.

Haplotype	WA				NSW
	C	G	P	O	H
1	2	11	10	30	-
2	1	-	-	-	-
3	6	1	2	-	-
4	6	7	2	-	-
5	2	-	3	-	-
6	1	3	1	-	-
7	5	7	2	-	-
8	1	-	-	-	-
9	1	-	1	-	-
10	1	1	2	-	-
11	1	-	-	-	-
12	1	-	1	-	-
13	1	-	-	-	-
14	1	1	3	-	-
15	-	2	2	-	-
16	-	2	-	-	-
17	-	1	-	-	-
18	-	1	-	-	-
19	-	-	4	-	-
20	-	-	1	-	-
21	-	-	-	-	2
22	-	-	-	-	2
23	-	-	-	-	1
n	30	37	34	30	5
n_H	14	11	13	1	3

5.3.2 Neutrality of the molecular marker

The results of the four neutrality tests, *i.e.* Tajima's (1989) test, Fu's (1997) F_S-test and Fu and Li's (1993) tests, for the control region fragment amplified in the present study are given in Table 5.4. These results show that the patterns of control region variation in the samples almost invariably conformed to expectations for a neutral sequence in mutation-drift

equilibrium. Only when Fu and Li's (1993) *D** test was applied to the Perth sample was there any evidence of significant departures from these expectations. However, the results of Fu and Li's (1993) *F** test, Tajima's (1989) test and Fu's (1997) F_S-test were not significant for the same sample (Table 5.4). The *D** test statistic is based on the difference between the number of singletons, *i.e.* mutations appearing only once among the sequences, and the total number of mutations (Fu and Li, 1993; see also Simonsen *et al*. 1995). Thus, since Perth was the only sample not to have any singletons, the relatively high values of Fu and Li's (1993) *D** were driven solely by the total number of mutations.

Table 5.4. Results of the neutrality tests conducted on the control region sequences for the four samples of *Argyrosomus japonicus* from Western Australia and the one sample from New South Wales. *D* = Tajima's (1989) neutrality statistic, F_S = Fu's (1997) neutrality statistic, *D** and *F** = Fu and Li's (1993) neutrality statistics. Statistically significant departures from neutral expectations, after the level of significance was corrected for multiple tests, are shown in bold. Sample sizes are given in Table 5.3. NA = not applicable (due to the sample from Oyster Harbour containing only a single haplotype).

Sample location	***D***	$\boldsymbol{F_S}$	***D****	***F****
Carnarvon	0.85 ($p > 0.10$)	-0.93 ($p > 0.10$)	0.51 ($p > 0.10$)	0.54 ($p > 0.10$)
Geraldton	1.27 ($p > 0.10$)	0.68 ($p > 0.10$)	0.29 ($p > 0.10$)	0.61 ($p > 0.10$)
Perth	1.24 ($p > 0.10$)	0.24 ($p > 0.10$)	**1.60 ($p < 0.02$)**	1.61 ($0.05 < p < 0.10$)
Oyster Harbour	0 ($p > 0.10$)	NA	NA	NA
Hawkesbury River (NSW)	-0.74 ($p > 0.10$)	1.96 ($p > 0.10$)	-0.19 ($p > 0.10$)	-0.20 ($p > 0.10$)

5.3.3 Genetic variation within geographic regions

Haplotype diversities for the samples from Carnarvon, Geraldton and Perth on the west coast were relatively high, with values ranging from 0.847 to 0.903 (Table 5.5). This high level of haplotype diversity reflects the fact that each of the west coast samples, comprising between 30 and 40 individuals, had between 11 and 14 different haplotypes

(Table 5.3). Nucleotide diversities for each of these west coast locations were moderate, *i.e.* 0.016 to 0.021 (Table 5.5), partly reflecting the presence of haplotypes that sometimes differed from each other by a relatively large number of mutational steps (see Fig. 5.3 later). In contrast, the levels of haplotype and nucleotide diversity in the control region fragment in the sample of *A. japonicus* obtained from Oyster Harbour on the south coast were zero (Table 5.5), which reflects the fact that all 30 individuals from this estuary had the same haplotype (Table 5.3).

Estimates of haplotype and nucleotide diversity for the sample of *A. japonicus* from the Hawkesbury River in New South Wales were 0.800 ± 0.164 and 0.012 ± 0.008, respectively (Table 5.5). While no detailed comparisons will be made, because of the low sample size, it should be noted that both haplotype and nucleotide diversity for the sample of *A. japonicus* obtained from the estuarine environment of the Hawkesbury River in New South Wales were more similar to those determined for the samples collected on the west coast, which were obtained from nearshore coastal waters, than those determined for the single estuary on the south coast, *i.e.* Oyster Harbour (Table 5.5).

The results of AMOVA indicate that most, *i.e.* 80.0%, of the control region variation found in the Western Australian samples of *A. japonicus* was within samples, which reflects the relatively high levels of haplotype diversity within these samples. The remaining 20.0% of variation was between samples and was significantly different from zero (p = 0.000), indicating the presence of a significant amount of heterogeneity in haplotype frequencies among sample locations. In addition, the standardised value of F_{ST} over all of the Western Australian samples was 0.613 and significantly different from zero (p = 0.000). When the sample from New South Wales was also considered, the overall percentage of variation within and among samples remained essentially unchanged, as did the value of the overall standardised F_{ST}.

Table 5.5. Summary of levels of genetic diversity in a 352-bp portion of the mtDNA control region for the four samples of *Argyrosomus japonicus* from Western Australia and the one sample from New South Wales. *n* = number of samples.

Sample location	*n*	Number of haplotypes	Number of polymorphic sites	Haplotype diversity *h* ± SD	Nucleotide diversity π ± SD
Carnarvon	30	14	24	0.903 ± 0.031	0.020 ± 0.011
Geraldton	37	11	19	0.847 ± 0.035	0.016 ± 0.009
Perth	34	13	22	0.890 ± 0.038	0.021 ± 0.011
Oyster Harbour	30	1	0	0	0
Hawkesbury River (NSW)	5	3	8	0.800 ± 0.164	0.012 ± 0.008

5.3.4 Genetic variation among geographic regions

The exact probability tests indicate that the haplotype frequencies in the three samples of *A. japonicus* from the west coast were not significantly different from each other (Table 5.6). However, it should be noted that the haplotype composition of the Carnarvon sample was significantly different from that of both Geraldton and Perth before the Bonferroni correction was applied, raising the possibility that there are relatively minor genetic differences between Carnarvon and these other populations. This significant result (prior to the Bonferroni correction) is partly due to the Carnarvon sample having the greatest number of unique haplotypes of all of the west coast samples and the fact that haplotype 3, which was the most common haplotype in the Carnarvon sample (20.0%), was poorly represented in both the Geraldton (2.7%) and Perth (5.9%) samples, while haplotype 1, which was the most common haplotype in the samples from Geraldton (29.7%) and Perth (29.4%), was poorly represented in the Carnarvon sample (6.7%) (Table 5.3). Each of the three samples from the west coast also contained three

or four haplotypes that were unique to that sample (Table 5.3). However, all but one of these haplotypes (and several other haplotypes as well) were rare, *i.e.* represented by a total of only one or two individuals (Table 5.3), and thus their geographic distributions are impossible to accurately characterise without recourse to unrealistically large sample sizes. The exact probability tests also indicate that the haplotype frequency in the sample from Oyster Harbour on the south coast was significantly different from those in the samples from the west coast locations of Carnarvon, Geraldton and Perth (Table 5.6). This was because all individuals in the Oyster Harbour sample had haplotype 1 and, although this haplotype was also present in all of the samples from the west coast, it was present at much lower frequencies (Table 5.3).

The exact tests also showed significant differences between the haplotype composition of the sample from the Hawkesbury River in New South Wales and that of each sample from Western Australia (Table 5.6). This result is driven by the fact that none of the three haplotypes present in the sample from New South Wales was found in any of the samples on the west coast (Table 5.3).

Table 5.6. Comparisons of the mtDNA control region haplotype frequency differences between pairs of samples of Australian *Argyrosomus japonicus*. The outcomes, *i.e. p* values, of exact probability tests for differences in haplotype frequencies between pairs of samples are shown. Statistically significant differences, after the level of significance was corrected for multiple tests, are shown in bold.

	Carnarvon	Geraldton	Perth	Oyster Harbour	Hawkesbury River (NSW)
Carnarvon	---				
Geraldton	$p = 0.029$	---			
Perth	$p = 0.027$	$p = 0.065$	---		
Oyster Harbour	***p* = 0.000**	***p* = 0.000**	***p* = 0.000**	---	
Hawkesbury River (NSW)	***p* = 0.003**	***p* = 0.000**	***p* = 0.000**	***p* = 0.000**	---

The patterns of distribution of the mtDNA control region sequence variation among the four samples of *A. japonicus* from Western Australia and the one sample from New South Wales have been summarised by plotting a multi-dimensional scaling (MDS) ordination of the standardised F_{ST} between pairs of samples (Fig. 5.2). The MDS ordination plot shows a clear distinction between the samples from Carnarvon, Geraldton and Perth on the west coast and that from Oyster Harbour on the south coast (Fig. 5.2). Furthermore, the west coast samples are grouped relatively close together, and particularly those from Geraldton and Perth (Fig. 5.2). The MDS plot also shows a clear distinction between all of the Western Australian samples and the sample from the Hawkesbury River in New South Wales (Fig. 5.2). However, it should be noted that, while the sample from Oyster Harbour on the south coast differed from those from Carnarvon, Geraldton and Perth, it was more similar to the west coast samples than to that from New South Wales. This reflects the fact that all Western Australian samples have haplotype 1, albeit at very different frequencies, and that this haplotype was not found in the single sample from New South Wales, although it should be recognised that the small size of the New South Wales sample would reduce opportunities for this

haplotype to be detected. Similarly, as noted above, none of the three haplotypes in the sample from New South Wales was found in those from Western Australia.

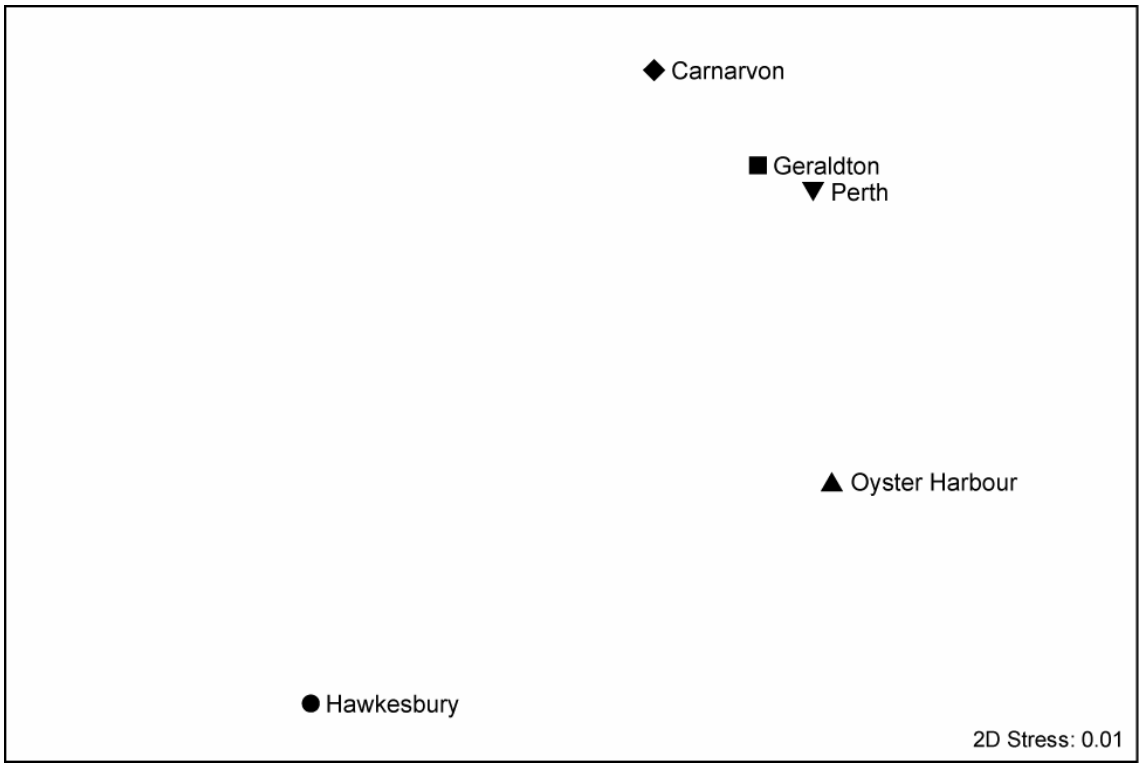


Figure 5.2. A two-dimensional ordination of standardised values of F_{ST}, based on variation in a 352bp portion of the mtDNA control region, between pairs of Australian samples of *Argyrosomus japonicus*.

5.3.5 Evolutionary relationships

Statistical parsimony analysis of the relationships among the partial control region haplotypes of *A. japonicus* from Carnarvon, Geraldton, Perth and Oyster Harbour in Western Australia and the Hawkesbury River in New South Wales, as well as the five South African haplotypes from the study of Klopper (2005) yielded two unconnected networks (Fig. 5.3). The first network comprised all Australian haplotypes, while the second comprised only the five South African haplotypes.

The total number of mutational steps in the Australian network is large, *i.e.* the overall amount of evolutionary divergence in *A. japonicus* in Australian waters is high

(Fig. 5.3). The number of possible haplotypes in the network is also large, although the network is characterised by numerous missing intermediate haplotypes, *i.e.* haplotypes that were not represented in the current samples (Fig. 5.3). These haplotypes may be missing because they have become extinct, *e.g.* via a population bottleneck, and/or because the sample sizes and geographic sampling was too limited for them to be detected. Regardless, groups of related haplotypes tended to be geographically widespread rather than confined to a particular location along the west coast (Fig. 5.3) and, as mentioned above, the sole haplotype in the Oyster Harbour sample was also found in each of the three west coast samples. Thus, although differences in the frequency distribution of haplotypes (discussed above) indicate the presence of population subdivision in *A. japonicus* in Western Australian waters, the lack of phylogeographic structure implies the presence of very recent genetic connections in *A. japonicus* between Oyster Harbour and Carnarvon in Western Australia. Furthermore, although the three haplotypes from the Hawkesbury River in New South Wales were all positioned in a similar part of the network, one of the west coast haplotypes (haplotype 5) fell within the range of variation represented by these New South Wales haplotypes (Fig. 5.3). Thus, although it is highly likely that *A. japonicus* is represented by different stocks on the west and east coasts of Australia (see above), these stocks do not appear to represent divergent evolutionary lineages. However, more extensive sampling of *A. japonicus* on both the east and south coasts of Australia in particular are needed to explore the evolutionary relationships between the west and east coast stocks of *A. japonicus*.

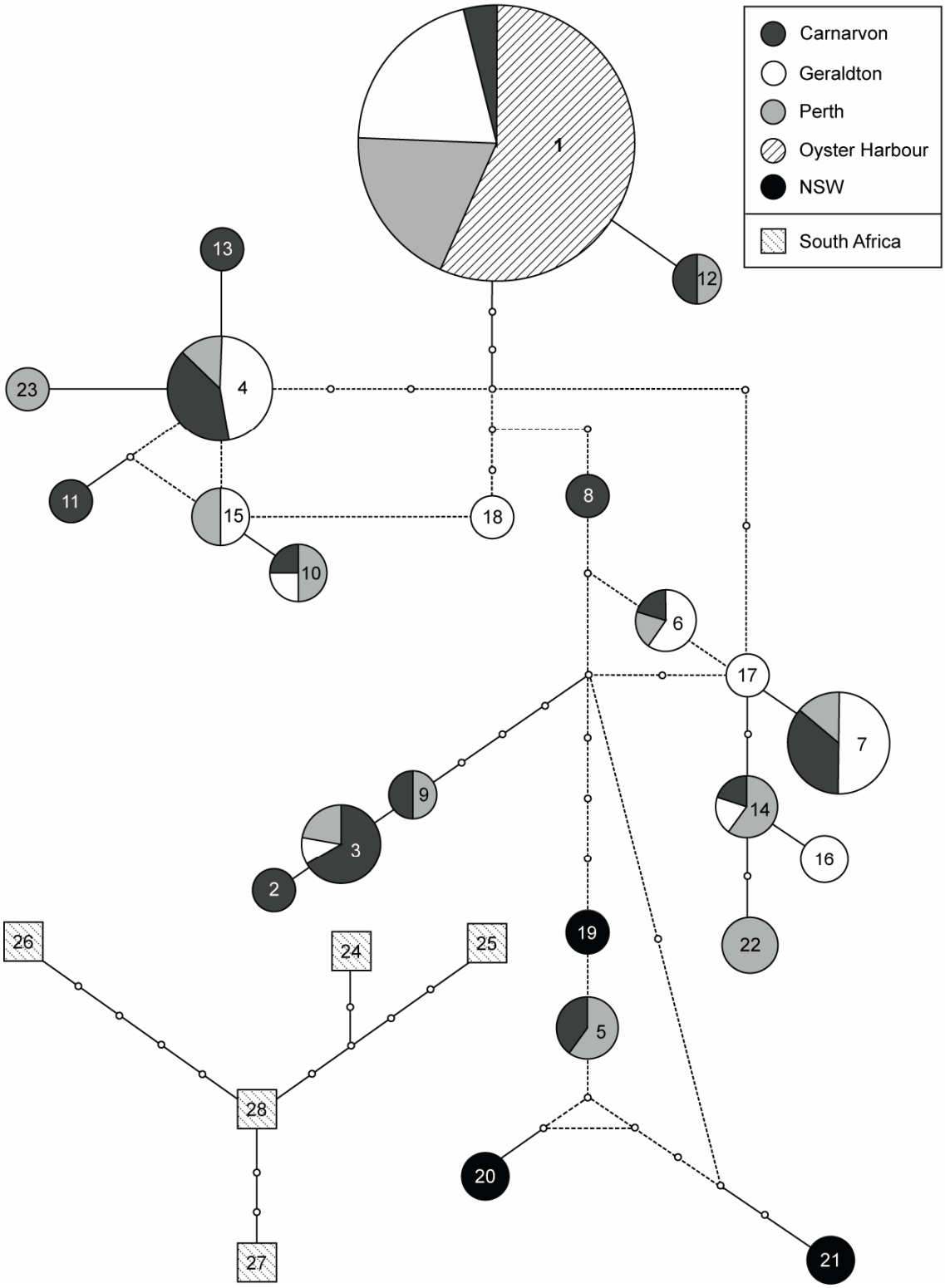


Figure 5.3. Haplotype network for the 23 Australian and 5 South African control region haplotypes of *Argyrosomus japonicus* obtained using the criterion of parsimony in TCS (version 1.21, Clement *et al*., 2000). The surface area of each circle or square is proportional to the number of individuals sharing that haplotype and each is allocated a colour/pattern that corresponds to the sample location. The numbers for Australian haplotypes are given in Tables 5.2 and 5.3, while the South African haplotypes are numbered from 24 to 28. Empty circles represent missing intermediate haplotypes and each line shows a single mutational change, regardless of its length. Dotted lines show the ambiguities present within the network.

In contrast to the situation on the west and east coasts of Australia, the minimum number of mutational steps between the South African and Australian haplotypes was 16. Furthermore, the genetic distance between haplotypes from each of these regions is large, with a maximum Kimura two parameter (K2P) value of 5.83% (and a mean K2P of 4.63%).

5.4 Discussion

5.4.1 Aspects of population genetic structuring in Western Australia

The results of the present study provide evidence of population subdivision in *A. japonicus* in Western Australia, particularly between the west and south coast populations. These populations differ not only in haplotype composition but also in their levels of genetic diversity. However, since these populations have a haplotype in common, they have probably been recently connected. The genetic distinction between the west and south coast populations is consistent with the biological differences in *A. japonicus* from these locations (see Chapters 3 and 4). There was also evidence of relatively minor genetic differences on the west coast, in particular between Carnarvon and the two assemblages on the lower west coast, *i.e.* Geraldton and Perth. Although larger sample sizes are required to confirm this, it does raise the possibility that, despite the general similarity in biological characteristics, more than one stock is represented on the west coast.

Population subdivision has commonly been detected in large sciaenids with similar life history characteristics to *A. japonicus*. While highly migratory, the adults of these larger sciaenids often form spawning aggregations in nearshore waters that are located in the vicinity of their natal estuary/embayment (*e.g.* Ramsey and Wakeman, 1987; Griffiths, 1996; Gold *et al*., 2001). The eggs/larvae resulting from these spawning events are often then retained within or near to that estuary/embayment, into which the early juveniles recruit. This pattern of natal homing has been hypothesised for South African *A. japonicus* (Griffiths, 1996), and population subdivision, possibly in the form of isolation by distance, has been detected for this sciaenid throughout that region (Klopper, 2005).

On the west coast, there was evidence of relatively minor genetic differences between Carnarvon and the two assemblages further south, *i.e.* Geraldton and Perth. The

relative distinctiveness of the Carnarvon sample from those of both Geraldton and Perth suggests that gene flow to and/or from the former population is restricted. It is thus relevant that there are a number of physical characteristics of the associated coastline that could aid in isolating the Carnarvon population. In particular, it may be unlikely for the eggs/larvae of *A. japonicus* to be advected from more southern locations into the north-facing and large marine embayment of Shark Bay, at the northern end of which Carnarvon is situated (Fig. 5.4). This may be particularly true as the rate of water exchange between Shark Bay and the open ocean is restricted (Logan and Cebulski, 1970; Nahas *et al*., 2005). However, since the nearshore waters of Carnarvon contain substantial numbers of early juvenile recruits and prespawning adults, *i.e.* with stage V gonads, were also caught in this region during the present study (*e.g.* Aylmore and Anderson, 2003; see also Chapter 4), spawning is likely to be occurring within Shark Bay. To the immediate south of Shark Bay and extending almost to Kalbarri is a stretch of high cliffs that are exposed to a heavy swell and have relatively deep waters at their base (Commonwealth of Australia, 2006). Since this stretch of coast lacks the shallow sheltered habitats in which the juveniles of *A. japonicus* are typically found (see Chapter 4), it is likely that individuals would be retained in Carnarvon/Shark Bay until maturity is attained. The subsequent spawning of these fish within their natal embayment could thus account for some genetic differentiation between this population and those of the lower west coast, *i.e.* Geraldton and Perth.

The lack of significant population structuring between Geraldton and Perth on the lower west coast may reflect a number of factors, which could include the physical characteristics of that coastline and the life history characteristics of this sciaenid. The nearshore coastal waters of the lower west coast are sheltered from offshore wave activity by a barrier of limestone reefs, shallow banks and islands (Masselink and Pattiaratchi, 2001). Since there are also few permanently-open estuaries along this coast,

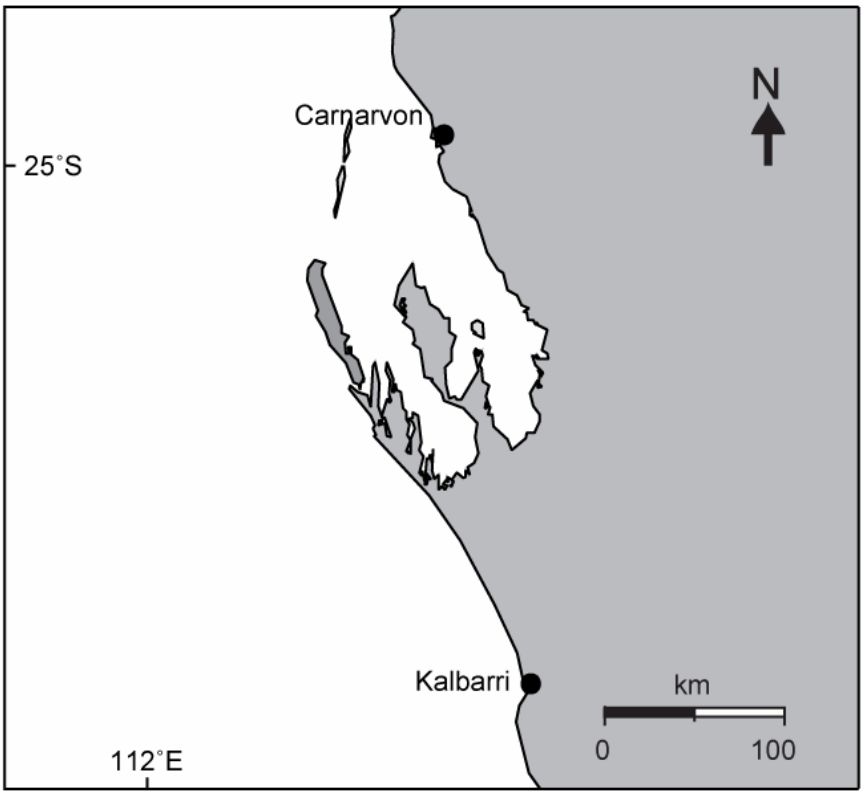


Figure 5.4. Map showing the location of Carnarvon and the orientation of Shark Bay.

juvenile *A. japonicus* frequently recruit into the nearshore coastal waters of this region (Farmer *et al*., 2005; see also Chapter 4). While the data available on movements are not adequate to draw conclusions on regional recruitment processes and patterns of juvenile dispersal, the lack of permanently-open estuaries or well defined marine embayments along much of this coast, particularly between Perth and Geraldton, would presumably increase the likelihood of mixing between the juveniles that recruit into these waters. Due to the relatively open nature of the habitat, the pelagic eggs of this species may also be advected long distances along this relatively straight coastline. Since tagging studies have also shown that adult *A. japonicus* are highly mobile and may cover distances in excess of 300 km on the west coast (Farmer, 2003), the migratory capabilities of adult fish may further reduce opportunities for local isolation and genetic divergence.

The results of this study of the population structure of *A. japonicus* in Western Australia are based on the patterns of variation in a single mitochondrial marker. This

type of marker is ideal for rapidly generating cost-effective but nevertheless highly informative data about the population genetic structure of a species (Avise, 1994), which was the main reasoning for its selection for this study. The main implications for the interpretation of data when using this particular type of marker are two-fold. First, the results are based upon a marker that typically shows strict maternal inheritance and therefore provides a measure of only female gene flow (Hutchinson *et al*., 1974; Avise and Vrijenhoek, 1987; May and Grewe, 1993). However, the available biological and tagging evidence provide no reason to expect the patterns of gene flow of the females and males of *A. japonicus* to differ (see Silberschneider and Gray, 2007), and thus the general findings are likely to have been the same, even if both female and male gene flow was considered. Second, since all of the assayed nucleotide positions are inherited as a single unit (Billington, 2003), the results provide only a single-locus estimate of population structure. This is potentially a problem because, for example, single-locus estimates of gene flow or of genetic diversity can be confounded by the effects of selection (Hauser and Ward, 1998), although the neutrality tests indicate that this is unlikely to be the case in the present *A. japonicus* data set.

The genetic composition of the sample from Oyster Harbour on the south coast differed from that of each west coast sample due to its possession of only a single haplotype. Except for the small isolated population in Oyster Harbour, *A. japonicus* is rarely encountered by recreational or commercial fishers in the nearshore coastal waters of Albany (Cusack and Roennfeldt, 2002; Coghlan, 2000; B. Farmer, pers. obs.). The apparent absence of this sciaenid from the coastal waters of Albany, *i.e.* outside Oyster Harbour, may be due to the high energy of that coastline and the lack of those neritic habitats which, on the west coast, are used as a nursery ground for the juveniles as well as a seasonal spawning ground for the adults (see Chapter 4). It is thus hypothesised that the population of *A. japonicus* in Oyster Harbour is likely to have originated through a

chance seeding of that estuary with eggs/larvae as a result of an uncharacteristic spawning event near to that system and/or due to atypical oceanographic conditions that transported eggs/larvae into the area. This hypothesis is consistent with the high prevalence of the Oyster Harbour haplotype, *i.e.* haplotype 1, on the lower west coast, which is in relatively close proximity to Oyster Harbour. However, more intensive sampling would be required to understand fully the range in the distribution of this particular haplotype. Since *A. japonicus* with pre-spawning (stage V) gonads were caught within Oyster Harbour during the present study, it is likely that spawning is occurring within or just outside this estuary. However, due to the lack of diversity in Oyster Harbour, it is likely that these local spawning events provide all of the recruitment into this system.

While the initial recruitment of *A. japonicus* into Oyster Harbour may have included a wider gene pool than present, genetic drift and inbreeding in that small population are likely to be the reason for the reduction in heterozygosity and a loss of alleles. Once a single allele becomes fixed in such a small isolated population, only mutation or gene flow from elsewhere can introduce new alleles (Allendorf and Luikart, 2007). It should be noted that, while *A. japonicus* appears to undergo an age- and/or size-related movement out of Oyster Harbour (see Chapter 4), with individuals of this population likely to be mixing with those in oceanic waters outside this system, gene flow must only be occurring in one direction. Although the absence of gene flow into the Oyster Harbour population is likely to be due to a lack of typical spawning habitat along the Albany coast (as mentioned previously), the physical characteristics of the estuary and its position in King George Sound may further aid in isolating this population. Although Oyster Harbour is a permanently-open estuary, it has a narrow entrance channel and is situated within the large marine embayment of King George Sound, which faces directly east (Fig. 5.5). Thus, even if larger adult *A. japonicus* were

spawning in the coastal waters near to Albany, the orientation of King George Sound may mean that the prevailing nearshore current, *i.e.* the West Wind Drift (Commonwealth of Australia, 2006), would advect larvae past that embayment, while the narrow entrance to Oyster Harbour would further reduce the likelihood of chance recruitment into this system (Fig. 5.5).

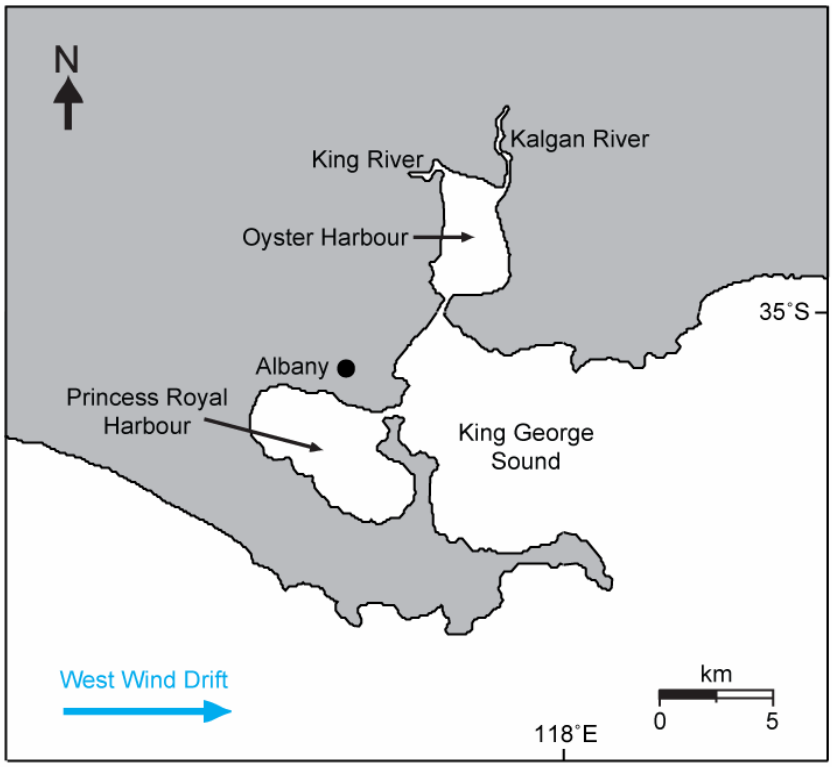


Figure 5.5. Map of the greater Albany area showing the location of Oyster Harbour in relation to King George Sound. The direction of the prevailing nearshore current, the West Wind Drift, is shown.

The sciaenid *Sciaenops ocellatus* is very similar to *A. japonicus* in terms of its life history characteristics and high capacity for dispersal in marine waters (*cf.* Murphy and Taylor, 1990; Seyoum *et al.*, 2000). During the study of Gold and Richardson (1994), a population of *S. ocellatus* that appeared to be reproductively isolated from all other Atlantic populations was identified. However, the reproductive isolation of this population proved to be transient, with no evidence of this isolation several years after it

was first detected (Seyoum *et al*., 2000). Thus, although no mtDNA control region diversity was detected among the *A. japonicus* in Oyster Harbour and this population currently appears to be reproductively isolated from all other populations, under certain conditions *A. japonicus* may be recruited from elsewhere into this permanently-open estuary. Given that the temporal stability of this situation is unknown, monitoring of genetic diversity in the Oyster Harbour population using non-lethal techniques, *e.g.* tagging and releasing fish while retaining only a small sample of scales or a segment of fin tissue, may be of value.

5.4.2 Morphological evidence of inbreeding in the Oyster Harbour population

Despite relatively high levels of diversity in the mtDNA control region of each of the west coast samples, the Oyster Harbour sample of *A. japonicus* contained no genetic diversity. As this sciaenid appears to spawn inside or near to Oyster Harbour, the latter lack of diversity raises the possibility that there is a high level of inbreeding in the Oyster Harbour population. This possibility is supported by observations of the morphology of individuals from this estuary. During biological examination, a number of deformities were detected among individuals of *A. japonicus* collected from Oyster Harbour on the south coast. Although deformities, which were only detected among the 0+ and 1+ age classes, primarily affected the nasal olfactory openings, deformities of the lower jaw, otoliths and operculum were also detected (Fig. 5.6). *Argyrosomus japonicus* normally possess a pair of olfactory nasal chambers that lie dorsolaterally in the mid-region of the snout and roughly in line with the eye. Each nasal chamber, which houses the olfactory receptor neurons, is connected to the external environment via two olfactory nasal openings (or nares), *i.e.* an anterior naris and a posterior naris (Fig. 5.6). In contrast, deformed fish had a single nasal opening on one or both side/s of their snout, which was due to these fish lacking the nasal bridge of epidermal tissue between

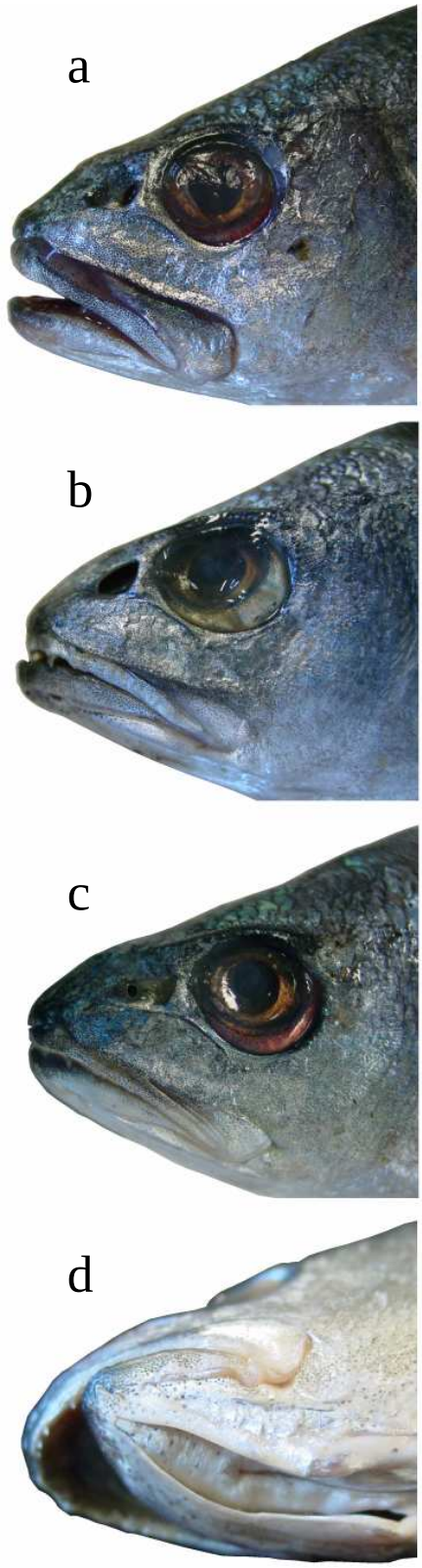


Figure 5.6. Examples of the morphological deformities observed among *Argyrosomus japonicus* collected from Oyster Harbour on the south coast. (a) The "normal" situation, with two nasal olfactory openings. (b) Single nasal olfactory opening due to the lack of nasal epidermal tissue that normally separates the anterior and posterior nares. (c). Single nasal olfactory opening due to nasal epidermal tissue covering the posterior naris. (d) An example of one of the more extreme deformities of the lower jaw.

the anterior and posterior nares or, less commonly, due to the posterior naris being covered by epidermal tissue (Fig. 5.6).

Preliminary estimates indicate that the most obvious deformities, *i.e.* those mentioned above and which were identifiable by eye, are present within this population at a frequency of *ca* 36% (n = 112). Since all *A. japonicus* from the west coast had been processed before sampling on the south coast had commenced, the frequency of occurrence of similar deformities could not be ascertained for the west coast samples. However, it should be noted that no deformities were detected during the biological examination of individuals from any of the west coast sampling localities. Thus, the high frequency at which these deformities were detected in the Oyster Harbour sample suggests that it reflects substantial inbreeding among the individuals found in this particular estuary. However, further sampling is required to determine both the temporal stability of this situation and to quantify fully the morphological deformities and/or asymmetries within this population. In particular, the effects of inbreeding on the developmental stability of *A. japonicus* should be more closely studied, which might involve the examination of selected bilateral traits for evidence of fluctuating asymmetry (*e.g.* Johnson *et al.*, 2004; Iguchi *et al.*, 2005).

There is now a considerable body of evidence that inbreeding has deleterious effects on fishes, which may include an increasing frequency of deformities, as well as decreased rates of growth and survival (*e.g.* Mtakovčić and Haley, 1979; Winemiller and Taylor, 1982; Kincaid, 1983, Wang *et al.*, 2002; Cena *et al.*, 2006). It is thus relevant that the rate of growth of *A. japonicus* was considerably slower in Oyster Harbour on the south coast than on the west coast (see Chapter 3), while the lack of deformities detected in the older age classes, *i.e.* 2+ to 4+, suggests that the survival of deformed individuals may be low. Since efficient water flow through and out of the epithelial chamber is a prerequisite for a functioning olfactory system (Hara and Law,

1972), the possession of a single nasal opening may significantly disrupt this system. Furthermore, the sensory epithelial area of cultured fish with a similar nasal deformity has been shown to be significantly less than in wild fish (Mana and Kawamura, 2002). Thus, reduced survival rates of deformed *A. japonicus* in Oyster Harbour may be associated with their relatively poor olfactory senses, which would lead to reduced feeding efficiency in the turbid estuarine waters or at night, *i.e.* when this sciaenid typically feeds (Hecht and Mperdempes, 2001), and particularly when competing with individuals that possess fully-functional olfactory systems. Since *A. japonicus* has been shown to be cannibalistic elsewhere (Griffiths, 1997a), the larger conspecifics in Oyster Harbour may then also favour the predation of deformed individuals, possibly due to their "dulled" senses or poorer conditioning.

In Japan, where Red Sea Bream *Pagrus major* and Black Sea Bream *Acanthopagrus schlegeli* are cultured for restocking programs, a similar nasal deformity has been detected at high frequencies among captive individuals of both of these species (Mana and Kawamura, 2002). While these authors were not able to determine whether the presence of a single naris per nasal chamber was genetically based or reflected environmental effects, the potential for inbreeding in aquaculture cannot be understated (see Wang *et al*., 2002). Furthermore, although deformed *P. major* and *A. schlegeli* generally outnumber "normal" individuals in the batches of fish used for restocking in Japanese waters, individuals with a single naris per nasal chamber are rarely seen post-release in the wild and this led to the hypothesis that deformed individuals had a low survival rate (Mana and Kawamura, 2002).

5.4.3 *Argyrosomus japonicus* elsewhere

The evidence from the mtDNA control region strongly suggests that the stocks of *A. japonicus* on the east and west coasts of Australia are genetically differentiated,

which is not surprising given the vast distances between those coastlines. The data also suggest, however, that the populations of *A. japonicus* on these two coasts were connected relatively recently. Although there are many marine species with genetically-differentiated, but closely related, west and east coast populations in southern Australia (*e.g.* MacDonald, 1980; Nurthen *et al.*, 1992; Meggs *et al.*, 2003), very little is generally known about their relationships and origins. The level of genetic divergence between the populations of *A. japonicus* in South Africa and Western Australia is much greater than was observed between any of the Australian populations, which implies that the populations on these different continents became separated much earlier. Indeed, the level of control region divergence between South African and Western Australian *A. japonicus* is even higher than is generally expected within a species, *i.e.* 1-2% (*e.g.* Alvarado Bremer *et al.*, 1997; Chen *et al.*, 1998; Kai *et al.*, 2004). It is thus possible that the *A. japonicus* on these continents represent separate species.

The presence of any species-level differences between *A. japonicus* populations in South Africa and Australia could be investigated further using the mtDNA gene cytochrome c oxidase subunit 1 (COI), which has already been used to correctly identify hundreds of Australian teleosts (Ward *et al.*, 2005), while revealing cryptic speciation in a wide range of animals (e.g. Herbert *et al.*, 2004; Smith *et al.*, 2006). However, it should also be kept in mind that some scientists are highly critical of deciding species boundaries solely on the basis of genetic distance estimates alone (Ebach and Holdredge, 2005; Will *et al.*, 2005). Furthermore, given the taxonomic uncertainty surrounding all four geographically-isolated populations of *A. japonicus* throughout the species worldwide distribution (see Chapter 1), future genetic studies should include samples from all of these locations. Since the type specimen of *A. japonicus* was caught in Japanese waters (Temminck and Schlegel, 1843), the discovery of any species-level differences between these populations will necessitate a revisiting of the scientific

nomenclature in all other regions. In this context, it is thus relevant that this sciaenid was first recorded from Australian waters by Castelnau (1872), who termed the individuals he described as *Sciaena antarctica*. It should be kept in mind that, regardless of whether the *A. japonicus* on each of these continents fulfils the criteria for a species, these geographically-isolated populations are clearly on different evolutionary pathways.

5.4.4 Future genetic research

The results of this chapter highlight three interrelated lines of research regarding the population structure of *A. japonicus* in Western Australia that would be highly desirable subjects for future research. First, in view of the likely presence of subtle genetic differences in *A. japonicus* on the west coast of Australia, it seems important to conduct a high resolution assessment of the population structure of this species in this region. Ideally, this study should involve the use of a large number of polymorphic nuclear loci to generate an information intensive data set. This, coupled with samples obtained from a greater number of locations along the west coast, should help to resolve the population genetic structure of *A. japonicus* on the west coast of Australia much more clearly than was possible in the current study. Second, the extent and implications of inbreeding in the population of *A. japonicus* in Oyster Harbour on the south coast requires further investigation, particularly since the discovery of inbreeding in a wild population of marine fish is relatively unusual. In addition, among other things, the resultant information should be useful for developing good practices for culturing this species, which is currently being targeted for mariculture. Finally, a study of the extent and patterns of genetic variation of *A. japonicus* across its broad geographic range would be useful from an academic perspective as it would contribute to a knowledge of the factors contributing to genetic divergence and promoting speciation in marine

environments and the time-scales over which these processes operate, which is currently an area of active research (*e.g.* Cavrilets *et al.*, 2007; Hubert *et al.*, 2007; Thacker *et al.*, 2007).

6.0 Management implications

6.1 Background and context

Declining fish stocks are a major problem for fisheries managers throughout the world (Jackson *et al.*, 2001; Pauly *et al*., 2002). Although commercial fishing has repeatedly been identified as a major cause for such declines (Botsford *et al*., 1997; Smith, 2002; Christensen *et al*., 2003; Hilborn *et al*., 2003; Pauly *et al*., 2003), the concept that recreational fisheries could also be contributing to those declines has been given much less attention (Cooke and Cowx, 2006). While there are fewer cases of declines in fish stocks being documented as due to recreational fishing, it may often be difficult to distinguish between the effects of the commercial and recreational sectors (Post *et al*., 2002). In countries with vast coastlines, such as Australia, the remote and diffuse nature of their recreational fisheries precludes rigorous monitoring programs and thus the net effect of this sector has often been overlooked (McPhee *et al*., 2002). Nevertheless, there are examples throughout the world where recreational fishing has been identified as a major factor contributing to declining fish stocks (*e.g.* Post *et al*., 2002; Coleman *et al.*, 2004). Thus, population growth and increased recreational fishing pressure pose specific challenges for the management of fisheries and, in particular, the setting of catch shares for the commercial and recreational fishing sectors.

Western Australia has a rapidly expanding population and increased recreational fishing pressure is of particular concern for the fisheries managers of this state (Fletcher and Head, 2006; Anon., 2007b). While shore fishing is popular in Western Australia, so too is offshore fishing and the number of recreational boats registered in this state between 2002 and 2006 increased steadily from 69166 to 81417 vessels (Anon., 2007b). Although it is recognised that not all boats registered in Western Australia would be used for recreational fishing, it is likely that a substantial portion of these would be used for that purpose. While increasing in number, recreational anglers are also continually improving their catch efficiency through improved technology, *e.g.* global positioning

systems, high quality colour echo-sounders and affordable underwater video systems, and improvements in angling gear, *e.g.* low-stretch gelspun and braided lines, fishing rod and reel designs and chemically-sharpened hooks. Furthermore, the availability of various forms of fishing media, *i.e.* books, magazines, television programs and internet forums, that are specific to the Western Australian coast provides relatively inexperienced anglers with instant access to generations of local fishing knowledge. A combination of the above factors, coupled with constraints on the growth of commercial fishing pressure, helps to account for estimates of the total annual recreational catch of some fish species in Western Australia, including *Argyrosomus japonicus*, now being greater than that of the commercial sector (see Chapter 1). Thus, in order to ensure that the fisheries resources of this state are sustained and appropriately shared, more stringent management regulations may be required for both recreational and commercial fishers.

Since Western Australia encompasses such a wide latitudinal range, within which the species composition, the biological characteristics of the species, fishing pressure and environmental conditions can vary markedly, commercial and recreational fishing are managed within four broad biological regions, *i.e.* Pilbara/ Kimberley, Gascoyne, West Coast and South Coast (Fletcher and Head, 2006). Although *A. japonicus* is relatively common in all but the Pilbara/Kimberley region, the regulations regarding the retention of this sciaenid are the same throughout the range of this species. In the case of both commercial and recreational fisheries, the minimum legal length for retention (MLL) of *A. japonicus* is 500 mm, while recreational fishers have a bag limit of two fish for any 24-hour period commencing at midnight. There are still certain species, including recreationally and commercially important species such as *A. japonicus*, for which adequate biological data were not available when current

management plans were formulated. In fact, the current research was implemented to address the inadequacy of biological data for *A. japonicus*.

6.2 Traditional biological considerations

6.2.1 Minimum legal length for retention

Limiting the size of individual fish that can be retained is a strategy commonly applied by fisheries managers as a mechanism for sustaining fish stocks. Indeed, MLLs have been used to manage various Australian fisheries for over a century and have proved a vital and effective method for conserving fish stocks (Hill, 1990; Winstanley, 1990). MLLs are generally based on the mean length at which 50% of the individuals of a given population first become sexually mature, *i.e.* the L_{50}, on the basis that this would enable a sufficient portion of the population to attain the size at maturity and thus potentially be able to spawn at least once prior to being harvested. The implementation of MLLs that are based on accurate and robust estimates of the size at which a species first matures can have a huge impact on the size and age structure of a population and thus enhance the potential egg production and recruitment of a fish stock (Rutherford, 2002).

The L_{50} at first maturity of the females and males of *A. japonicus* on the west coast were 903 and 880 mm, respectively, these lengths typically being reached at *ca* 4.5 and 5 years of age. Since the current MLL for the retention of *A. japonicus* in Western Australian waters is only 500 mm and well below the L_{50}s of both females and males at first maturity on the west coast, many fish in this region will be caught and retained before they have had the opportunity to spawn. While an increase in MLL in line with the L_{50} determined for females on the west coast, *i.e. ca* 900 mm, could be considered appropriate, there are a number of interrelated factors that require careful consideration. For example, an increase in MLL may have a detrimental economic

impact on commercial fishers that catch relatively large numbers of *A. japonicus* along the west coast and it may exclude the majority of recreational anglers from catching fish of legal size outside the spawning season when fish > L_{50} live predominantly in deeper offshore waters. However, any impacts to commercial or recreational fishing may only be short term or seasonal and the benefits are likely to far outweigh any potential losses. For example, since growth from the current MLL of 500 mm to a length of 900 mm would take only two to three years, the larger average size of fish has the potential to provide greater catches in terms of weight for the commercial sector and better angling experiences for the recreational sector.

If a substantial increase in the MLL was to be implemented, the level of mortality associated with the handling and release of undersize fish would also have to be considered. Much of the available evidence suggests that *A. japonicus* is relatively sensitive to handling and stress, which generally equates to high rates of mortality upon interaction with fishing gears (Gray, 2002). However, the level of mortality associated with capture by the most commonly used recreational fishing gear, *i.e.* rod and line, appears to be low, particularly if fish are hooked in the mouth and retrieved from relatively shallow depths, *i.e.* < 2 m (Broadhurst and Barker, 2000). Since the survival of fish released after capture by a similar method has been shown to depend on both the anatomical location of the hook as well as handling techniques (Butcher *et al*., 2007), raising public awareness of the most appropriate handling and release practices should also be considered. While there have been reports of juvenile *A. japonicus* being discarded as bycatch in a number of commercial fisheries in New South Wales, and particularly by the estuarine prawn trawl fishery (Gray *et al*., 1990; Broadhurst and Kennelly, 1994, 1995), similar techniques do not tend to catch large numbers of juvenile *A. japonicus* in Western Australia.

The females and males of *A. japonicus* in Oyster Harbour on the south coast of Western Australia attained maturity at a far smaller size and younger age than on the west coast. As the L_{50}s of both female and male *A. japonicus* in Oyster Harbour were 493 and 419 mm, respectively, and were thus below the current MLL of 500 mm, the majority of fish in this population would potentially have the opportunity to spawn at least once prior to being retained. Furthermore, since small *A. japonicus* are not regarded as a quality food fish in Western Australia (Cusack and Roennfeldt, 2002), the vast majority of the fish caught in this estuary are released (B. Farmer, pers. obs.). Thus, while the current MLL of 500 mm appears to be appropriate for conserving the population of *A. japonicus* in Oyster Harbour, the extremely low level of genetic diversity within this estuarine population provides an additional and unique risk factor that requires further consideration (see section 6.2.3).

6.2.2 Temporal and spatial closures to fishing

Temporal and spatial closures of key spawning areas to fishing have been used to manage exploited fish populations (Sadovy, 1996; Jennings *et al*., 2001). Fish are often more vulnerable to capture during their spawning period because of their particular behavioural characteristics at that time. These characteristics can include the formation of dense aggregations in nearshore waters and increased vocal activity, *e.g.* the croaking or drumming noises made by many sciaenids as part of their courtship behaviour (Connaughton and Taylor, 1995; Luczkovich *et al*., 1999; Holt, 2002; Lagadère and Mariani, 2006; Ueng *et al*., 2007). As with MLLs, the temporal and spatial protection of spawning fish helps conserve adult stocks and thus enhances egg production and the level of recruitment to a fishery.

During the present study, the lower reaches of the Swan River Estuary, *i.e.* Mosman Bay, were identified as a spawning ground for *A. japonicus* on the lower west

coast. While spawning is hypothesised to occur predominantly in discrete spawning aggregations in the nearshore coastal waters of the west coast, the Swan River aggregations are unique in that they occur within an estuary. The seasonal presence of large fish in the lower reaches of the Swan River Estuary has long been known, with the annual commercial catch of *A. japonicus* from this system between 1912 and 1974 averaging 1.5 tonnes (Riggert, 1978). Commercial fishing for *A. japonicus* in the Swan River has declined in recent years, with the average annual catch from the Swan River between 1995 and 2004 being only 173 kg.

Despite a reduction in commercial fishing in the Swan River, the seasonal aggregations of adult *A. japonicus* have become an increasingly popular target for recreational anglers and the catches taken by this sector now exceed those of the commercial fishery (Malseed and Sumner, 2001; Smith, 2006; see Section 1.4.4). Furthermore, since the presence of large *A. japonicus* seasonally in Mosman Bay was identified as a spawning aggregation in various fishing media, there has been an increase in the numbers of people targeting these fish for catch and release, albeit with limited success (see section 6.2.4). As the Swan River is situated on the most densely-populated stretch of coast in Western Australia and is easily accessible to even the modestly-equipped angler, this particular aggregation may need to be accorded additional protection during the main spawning period of this sciaenid on the lower west coast, *i.e.* November to February.

6.3 Population genetic considerations

The population of *A. japonicus* in Oyster Harbour on the south coast was genetically very different to those of the west coast, which was due to the presence of only a single haplotype in the population in that estuarine locality. The low level of genetic diversity in the Oyster Harbour population of *A. japonicus* is likely to have been due to genetic

drift and inbreeding in a small isolated population, which may have been founded by only a very limited number of recruits. Once a single allele becomes fixed in such a small isolated population, only mutation or gene flow from elsewhere, *i.e.* either naturally or through human intervention, can introduce new alleles (Allendorf and Luikart, 2007). However, even if *A. japonicus* was introduced into Oyster Harbour in an attempt to expand the currently limited gene pool, or if mutations arose, it is likely that any additional variation would be lost over time due to the effects of genetic drift in that small population. Since Oyster Harbour is a permanently-open estuary, the reproductive isolation of this population may be only temporary and thus, although unlikely, the problem of low genetic diversity and the effects of inbreeding may be overcome naturally under certain circumstances.

Despite the extremely low levels of genetic diversity, the fact that substantial numbers of *A. japonicus* are present in Oyster Harbour suggests that the level of mortality associated with inbreeding does not prevent significant numbers of fish from attaining maturity and thus providing continued recruitment to that system (Hoeksema and Chuwen, unpubl. data). Furthermore, since few *A. japonicus* are currently caught commercially in Oyster Harbour and the majority of fish caught by recreational anglers are released (Smith *et al*., 2006; B. Farmer, pers. obs.), mortality associated with fishing is presumably low. Thus, while the population of *A. japonicus* in Oyster Harbour is likely to persist into the near future, the lack of genetic diversity in this population reduces its capability for adaptation and thus increases the risk of local extinction (*e.g.* Frankham, 1995; Landweber and Dobson, 1999; Allendorf and Luikart, 2007). Adaptation is a response to selection pressure that requires genetically-based phenotypic diversity and without such diversity an evolutionary response is not possible (Allendorf and Luikart, 2007). Thus, while no changes to management are proposed for

A. japonicus in Oyster Harbour at the present time, this unique and vulnerable population should be closely monitored.

The genetic component of the present study raised further implications for management, which included the following. 1) On the basis of the compositions of the mtDNA haplotypes of *A. japonicus*, it is concluded that the assemblages from Carnarvon on the upper west coast are genetically distinct from those of both Geraldton and Perth on the lower west coast, which are similar. While there are currently no biological differences between these stocks, future differences are likely given their partial reproductive isolation, and these populations should be managed accordingly. 2) Since the level of divergence between South African and Western Australian *A. japonicus* is high, implying a relatively long separation of these stocks, fisheries managers should exercise caution in using data collected for South African populations when considering management plans for populations in Western Australia. 3) The occurrence of inbreeding in the Albany population highlights the need to ensure a large genetically-diverse broodstock when using *A. japonicus* for aquaculture and particularly if this species is considered for restocking wild populations.

6.4 Other considerations

Primarily due to ease of access, the stocks of fish in the nearshore waters of Perth in Western Australia are becoming depleted (Fletcher and Head, 2006; Anon., 2007b). As a result, boat-based recreational anglers are venturing further offshore each year and are now regularly fishing in water depths in excess of 100 m (Anon., 2007b). While many recreational anglers fishing in these depths are sport fishers, *i.e.* who fish primarily for catch and release, and for which Samson Fish *Seriola hippos* is their primary target, these anglers regularly come across other species, including schools of mature *A. japonicus* (A. Bevan, Shikari Charters, pers. comm.; B. Farmer, pers. obs.). While

S. hippos survives well following retrieval from depth and subsequent release, this is not the case with *A. japonicus*, which is generally near death upon landing (A. Bevan, Shikari Charters, pers. comm.; B. Farmer, pers. obs.). Given that release is out of the question for *A. japonicus* caught at these depths, it could be argued that this species should not be considered a sport fishing target in those waters. Sport fishing has also extended to the spawning aggregations in the Swan River, where people have been targeting these large mature fish for tag and release. The collection of five dead fish from the shallows of the lower reaches of the Swan River following their capture, tagging and release on the previous night, suggests that mortality following capture even at moderate depths of 15-20 m is considerable. The problem of high levels of release mortality in the Swan River has been highlighted recently in the fishing media (Coghlan, 2007), and sport fishing in this locality should be further discouraged. Thus, the proposed closure to fishing of this sciaenid in Mosman Bay during the spawning period on the lower west coast should extend to all forms of fishing, *i.e.* whether it is for food or sport.

6.5 The Sciaenidae, a broader perspective

The biological, ecological and fishery characteristics that typify the majority of larger sciaenids (*i.e.* with maximum lengths > 1 m) make them especially vulnerable to exploitation. Although these larger members of the family are highly fecund, a trait which should provide their stocks with added resilience when facing heavy exploitation, there are numerous examples that highlight their vulnerability to fishing. While the case studies of *Bahaba taipingensis* and *Totoaba macdonaldi* have been the most publicised (*e.g.* Sadovy and Cheung, 2003; see also Chapter 1), similar patterns of overexploitation are a common feature of large sciaenids throughout the world (Kawasaki, 1987; James, 1994; Griffiths, 1996, 1997b; Pitcher *et al.*, 1998; Wolff, 2000a, 2000b). Since

A. japonicus in Western Australian waters share with these large sciaenids a similar suite of biological, ecological and fishery characteristics, they too should be considered especially vulnerable to exploitation. Thus, the formulation of a rational management plan that is based on sound biological data for *A. japonicus* in Western Australian waters should be considered a high priority for the fisheries managers of this state.

References

Abascal, F.J., Medina, A., Megina, C. and Calzada, A. (2002). Ultrastructure of *Thunnus thynnus* and *Euthynnus alletteratus* spermatozoa. *Journal of Fish Biology* **60**: 147-153.

Aboim, M.A., Menezes, G.M., Schlitt, T. and Rogers, A.D. (2005). Genetic structure and history of populations of the deep-sea fish *Helicolenus dactylopterus* (Delaroche, 1809) inferred from mtDNA sequence analysis. *Molecular Ecology* **14**: 1343-1354.

Abookire, A.A. and Macewicz, B.J. (2003). Latitudinal variation in reproductive biology and growth of female Dover sole (*Microstomus pacificus*) in the North Pacific, with emphasis on the Gulf of Alaska stock. *Journal of Sea Research* **50**: 187-197.

Acha, E.M., Mianzan, H., Lasta, C.A. and Guerrero, R. (1999). Estuarine spawning of the whitemouth croaker *Micropogonias furnieri* in the Rio de la Plata, Argentina. *Marine and Freshwater Research* **50**: 57-65.

Agrawal, A.A. (2001). Phenotypic plasticity in the interactions and evolution of species. *Science* **294**: 321-326.

Aguileira, S.O.A. (1982). *Musculatura facial em peces Sciaenidae del atlantico oeste y rio de Amazonica*. Unpublished Masters Thesis, University de Oriente. Cumana, Venezuela.

Aguilera, O. and Rodrigues de Aguilera, D. (2003). Two new otolith based sciaenid species of the genus *Plagioscion* from South American Neogene marine sediments. *Journal of Palaeontology* **77**: 1133-1138.

Allendorf, F.W. and Luikart, G. (2007).*Conservation and the Genetics of Populations*. Blackwell Publishing, Carlton.

Alvarado Bremer, J.R., Naseri, I. and Ely, B. (1997). Orthodox and unorthodox phylogenetic relationships among tunas revealed by the nucleotide sequence analysis of the mitochondrial DNA control region. *Journal of Fish Biology* **50**: 540-554.

Anon. (1981). *Amateur angling in Botany Bay*. Report No. BBS 24. State Pollution Control Commission, Sydney.

Anon. (1993). Mulloway (*Argyrosomus hololepidotus*). *Fishing WA* **2**: 1-4. Department of Fisheries, Perth.

Anon. (1996). *Shark Bay Marine Reserves Management Plan (1996-2000).* Department of Conservation and Land Management. Perth.

Anon. (2003). Relationships between river flows and commercial fish catches in the Hawkesbury-Nepean and Shoalhaven River systems. Hawkesbury-Nepean River Management Forum.

Anon. (2007a). *Size, take and possession limits: Tidal waters*. Department of Primary Industries and Fisheries, Queensland Government.

Anon. (2007b). *Managing of the recreational catch of demersal scalefish on the west coast*. Fisheries management paper No. 225. Western Australian Department of Fisheries, Perth.

Apte, S. and Gardner, J.P. (2002). Population genetic subdivision in the New Zealand greenshell mussel (*Perna canaliculus*) inferred from single-strand conformation polymorphism analysis of mitochondrial DNA. *Molecular Ecology* **11**: 1617-1628.

Avise, J.C. (1994). *Molecular Markers, Natural History and Evolution*. Chapman and Hall, New York.

Avise, J.C. and Vrijenhoek, R.C. (1987). Mode of inheritance and variation of mitochondrial DNA in hybridogenetic fishes of the genus *Poeciliopsis*. *Molecular Biology and Evolution* **4**: 514-525.

Aylmore, S. and Anderson, S. (2003). *Plan of Management for the Miaboolya Beach Fish Habitat Protection Area.* Fisheries Management Paper No. 161. Department of Fisheries, Perth.

Ayvazian, S.G., Johnson, M.S., McGlashan, D.J. (1994). High levels of genetic subdivision of marine and estuarine populations of the estuarine catfish *Cnidoglanis macrocephalus* (Plotosidae) in south-western Australia. *Marine Biology* **118**: 25-31.

Baccetti, B., Burrini, A.G., Callini, G., Gibertini, G., Mazzini, M. and Zerunian, S. (1984). Fish germinal cells. I. Comparative spermatology of seven cyprinid species. *Gamete Research* **10**: 373-396.

Bagenal, T.B. and Tesch, F.W. (1978). Age and growth. In: *Methods for Assessment of Fish Production in Fresh Waters* (Bagenal, T.B., Ed.). pp. 101-136. Blackwell Scientific, London.

Ballard, J.W.O. and Whitlock, M.C. (2004). The incomplete natural history of mitochondria. *Molecular Ecology* **13**: 729-744.

Barbieri, L.R., Chitterden Jr, M.E. and Lowerre-Barbieri, S.K. (1994). Maturity, spawning and ovarian cycle of Atlantic croaker, *Micropogonias undulates*, in Chesapeake Bay and adjacent coastal waters. *Fishery Bulletin* **92**: 671-685.

Barnes, M.A. and Power, G. (1984). A comparison of otolith and scale ages for western Labrador lake whitefish, *Coregonus clupeaformis*. *Environmental Biology of Fishes* **10:** 297-299.

Barrera-Guevara, J.C. (1990). The conservation of *Totoaba macdonaldi* (Gilbert), (Pisces: Sciaenidae), in the Gulf of California, Mexico. *Journal of Fish Biology* **37**(Suppl. A): 201-202.

Barros, N.B., Jefferson, T.A. and Parsons, E.C.M. (2004). Feeding habits of Indo-Pacific Humpback Dolphins (*Sousa chinensis*) stranded in Hong Kong. *Aquatic Mammals* **30**: 179-188.

Barton, M. (2007). *Bond's Biology of Fishes* (3rd edition). Thomson, Belmont, California.

Battaglene, S.C. (1996). Hatchery production of juvenile snapper and mulloway. In: *Marine finfish farming – Proceedings of a workshop* (Quartararo, N., Ed.). New South Wales Fisheries Research Institute, Cronulla.

Battaglene, S.C. and Talbot, B.R. (1994). Hormone induction and larval rearing of mulloway, *Argyrosomus japonicus* (Pisces: Sciaenidae). *Aquaculture* **126**: 73-81.

Beamish, R.J. (1979). New information on the longevity of Pacific ocean perch (*Sebastes alutus*). *Journal of the Fisheries Research Board of Canada* **36**: 1395-1400.

Beamish, R.J. and Fournier, D.A. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 982-983.

Beamish, R.J. and McFarlane, G.A. (1983). The forgotten requirement for age validation in fisheries biology. *Transactions of the American Fisheries Society* **112**: 735-743.

Beamish, R.J. and McFarlane, G.A. (1987). Current trends in age determination methodology. In: *Age and Growth of Fish* (Summerfelt, R.C. and Hall, G.E., Eds). *pp*. 15-42. Iowa State University Press, Ames.

Beheregaray, L.B. and Sunnucks, P. (2001). Fine-scale genetic structure, estuarine colonisation and incipient speciation in the marine silverside fish *Odontesthes argentinensis. Molecular Ecology* **10**: 2849-2866.

Beauchamp, J.J. and Olson, J.S. (1973). Corrections for bias in regression estimates after logarithmic transformation. *Ecology* **54**: 1403-1407.

Beckman, D.W. and Wilson, C.A. (1995). Seasonal timing of opaque zone formation in fish otoliths. In: *Recent Developments in Fish Otolith Research* (Secor, D.H., Dean, J.M., Campana, S.E. and Miller, A.B., Eds). *pp*. 27-41. University of South Carolina Press, Columbia.

Beckman, D.W., Wilson, C.A. and Stanley, A.L. (1989). Age and growth of red drum, *Sciaenops ocellatus*, from offshore waters of the northern Gulf of Mexico. *Fishery Bulletin* **87**: 17-28.

Belk, M.C. (1995). Variation in growth and age at maturity in bluegill sunfish: genetic or environmental effects? *Journal of Fish Biology* **47**: 237-247.

Belk, M.C. (1998). Predator-induced delayed maturity in bluegill sunfish (*Lepomis macrochirus*): variation among populations. *Oecologia* **113**: 203-209.

Berasategui, A.D., Acha, E.M. and Fernandez Araoz, N.C. (2004). Spatial patterns of ichthyoplankton assemblages in the Rio de la Plata Estuary (Argentina-Uruguay). *Estuarine, Coastal and Shelf Science* **60**: 599-610.

Berg, L.S. (1958). System der rezenten und fossilen Fischartigen und Fische. VEB Verlag der Wissenschaften, Berlin.

Bethea, D.M., Buckel, J.A. and Carlson, J.K. (2004). Foraging ecology of the early life stages of four sympatric shark species. *Marine Ecology Progress Series* **268**: 245-264.

Beverton, R.J.H. and Holt, S.J. (1957). *On the Dynamics of Exploited Fish Populations*. Chapman and Hall, London.

Bialetzki, A., Nakatani, K., Sanches, P.V. and Baumagartner, G. (2004). Eggs and larvae of the 'curvina' *Plagioscion squamosissimus* (Heckel, 1840) (Osteichthyes, Sciaenidae) in the Baia River, Mato Grosso do Sul State, Brazil. *Journal of Plankton Research* **26**: 1327-1336.

Billington, N. (2003). Mitochondrial DNA. In: *Population Genetics: Principles and Applications for Fisheries Scientists* (Hallerman, E.M., Ed.). *pp*. 59-100. American Fisheries Society, Bethesda.

Bilodeau, A.L., Felder, D.L. and Neigel, J.E. (2005). Population structure at two geographic scales in the burrowing crustacean *Callichirus islagrande* (Decapoda, Thalassinidea): historical and contemporary barriers to planktonic dispersal. *Evolution* **59**: 2125-2138.

Blaber, S.J.M. (2000). *Tropical Estuarine Fishes. Ecology, Exploitation and Conservation*. Blackwell Science, Carlton.

Blaber, S.J.M. and Blaber, T.G. (1980). Factors affecting the distribution of juvenile estuarine and inshore fish. *Journal of Fish Biology* **17**: 143-162.

Blaber, S.J.M., Brewer, D.T., Salini, J.P. and Kerr, J. (1990). Biomasses, catch rates and abundances of demersal fishes, particularly predators of prawns, in a tropical bay in the Gulf of Carpentaria, Australia. *Marine Biology* **107**: 397-408.

Black, M. and Dixon, P.I. (1992). Stock identification and discrimination of Mulloway in Australian waters (FIRTA 86/16). The University of New South Wales, Sydney.

Black, R., Robertson, A.I., Peterson, C.H. and Peterson, N.M. (1990). Fishes and benthos of near-shore seagrass and sand flat habitats at Monkey Mia, Shark Bay, Western Australia. In: *Research in Shark Bay, Report of the France-Australe Bicentenary Expedition Committee* (Berry, P.F., Bradshaw, S.D. and Wilson, B.R., Eds). *pp.* 245-261. Western Australian Museum, Perth.

Blacker, R.W. (1974). Recent advances in otolith studies. In: *Sea Fisheries Research* (Harden Jones, F.R., Ed.). *pp*. 67-90. Elek Science, London.

Boeger, W.A. and Kritsky, D.C. (2003). Parasites, fossils and geologic history: Historical biogeography of the South American freshwater croakers *Plagioscion* spp. (Teleostei, Sciaenidae). *Zoologica scripta* **32**: 3-11.

Boehlert, G.W. (1985). Using objective criteria and multiple regression models for age determination in fishes. *Fishery Bulletin* **83**: 103-117.

Booth, A.J., Merron, G.S. and Buxton, C.D. (1995). The growth of *Oreochromis andersonii* (Pisces: Cichlidae) from the Okavango Delta, Botswana, and a comparison of the scale and otolith methods of ageing. *Environmental Biology of Fishes* **43**: 171-178.

Borsa, P. (2002). Allozyme, mitochondrial-DNA and morphometric variability indicate cryptic species of anchovy (Engraulis encracicolus). *Biological Journal of the Linnean Society* **75**: 261-265.

Botsford, L.W., Castilla, J.C. and Peterson, C.H. (1997). The management of fisheries and marine ecosystems. *Science* **277**: 509–515.

Brearley, A. (2005). *Ernest Hodgkin's Swanland: Estuaries and Coastal Lagoons of South-western Australia*. University of Western Australia Press. Crawley.

Broadhurst, M.K. and Barker, D.T. (2000). Effects of capture by hook and line on plasma cortisol, scale loss and survival in juvenile mulloway, *Argyrosomus hololepidotus*. *Archive of Fishery and Marine Research* **48**: 1-10.

Broadhurst, M.K. and Kennelly, S.J. (1994). Reducing the by-catch of juvenile fish (mulloway *Argyrosomus hololepidotus*) using square-mesh panels in codends in the Hawkesbury River prawn-trawl fishery, Australia. *Fisheries Research* **19**: 321-331.

Broadhurst, M.K. and Kennelly, S.J. (1995). A trouser-trawl experiment to assess the codends that exclude juvenile mulloway (*Argyrosomus hololepidotus*) in the Hawkesbury River prawn trawl fishery. *Marine and Freshwater Research* **46**: 953-958.

Bromage, N.R., Randall, C., Thrush, M. and Duston, J. (1993). The control of spawning in salmonids. In: *Recent Advances in Aquaculture (vol. 4)* (Roberts, R.J. and Muir, J., Eds). *pp.* 55-65. Blackwell Science, Oxford.

Brown, N.P., Bromage, N.R. and Shields, R.J. (1995). The effect of spawning temperature on egg viability in the Atlantic halibut (*Hippoglossus hippoglossus*) In: *Reproductive Physiology of Fish, Proceedings of the Fifth International Symposium, July 2-8, 1995, Austin, Texas. pp.* 181.

Brown, W.M. (1983). Evolution of animal mitochondrial DNAs. In: *Evolution of Genes and Proteins* (Nei, M. and Koehn, R.K., Eds). *pp*. 62-88. Sinauer, Sunderland.

Brown-Peterson, N.J. and Thomas, P. (1988). Differing reproductive life histories between temperate and subtropical groups of *Cynoscion nebulosus*. *Contributions in Marine Science* **30**(Supplement): 71-78.

Brown-Peterson, N.J., Peterson, M.S., Nieland, D.L., Murphy, M.D., Taylor, R.G. and Warren, J.R. (2002). Reproductive biology of female spotted seatrout, *Cynoscion nebulosus*, in the Gulf of Mexico: differences among estuaries? *Environmental Biology of Fishes* **63**: 405-415.

Burling, M.C., Pattiaratchi, C.B and Ivey, G.N.(2003). The tidal regime of Shark Bay, Western Australia. *Estuarine, Coastal and Shelf Science* **57**: 725-735.

Burns, J.R., Weitzman, S.H., Lange, K.R., Malabarba, L.R. (1998). Sperm ultrastructure in characid fishes (Teleostei Ostariophysi). In: *Phylogeny and Classification of Neotropical Fishes* (Malabarba, L.R., Reis, R.E., Vari, R.P., Lucena, Z.M.S. and Lucena, C.A.S., Eds). *pp*. 235-244. EDIPUCRS, Porto Alegre.

Butcher, P.A., Broadhurst, M.K., Reynolds, D., Reid, D.D. and Gray, C.A. (2007). Release method and anatomical hook location: effects on short-term mortality of angler-caught *Acanthopagrus australis* and *Argyrosomus japonicus*. *Diseases of Aquatic Organisms* **74**: 17-26.

Buxton, C.D. and Clarke, J.R. (1989). The growth of *Cymatoceps nasutus* (Teleostei: Sparidae) with comments on diet and reproduction. *South African Journal of Marine Science* **8**: 57-65.

Cailliet, G.M., Radtke, R.L. and Weldon, B.A. (1986). Elasmobranch age determination and verification: a review. In: *Indo-Pacific Fish Biology: Proceedings of the Second International Conference on Indo-Pacific Fishes* (Uyeno, T., Arai, R., Taniuchi, T. and Matsuura, K., Eds). *pp*. 345-360.

Campana, S.E. (1999). Chemistry and composition of fish otoliths: pathways, mechanisms and applications. *Marine Ecology Progress Series* **188**: 263-297.

Campana, S.E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**: 197-242.

Campana, S.E. and Casselman, J.M. (1993). Stock discrimination using otolith shape analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **50**: 1062-1083.

Campana, S.E. and Moksness, E. (1991). Accuracy and precision of age and hatch date estimates from otolith microstructure examination. *ICES Journal of Marine Science* **48**: 303-316.

Campana, S.E. and Thorrold, S.R. (2001). Otoliths, increments, and elements: keys to a comprehensive understanding of fish populations? *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 30-38.

Campana, S.E., Zwanenberg, K.C.T. and Smith, J.N. (1990). $^{210}Pb/^{226}Ra$ determination of longevity in redfish. *Canadian Journal of Fisheries and Aquatic Sciences* **47**: 163-165.

Carvalho, G.R. and Hauser, L. (1994). Molecular genetics and the stock concept in fisheries. *Review of Fish Biology and Fisheries* **4**: 326-350.

Casatti, L. (2003). Family Sciaenidae (drums or croakers). In: *Check List of the Freshwater Fishes of South and Central America* (Reis, R.E., Kullander, S.O., Ferraris Jr., C.J., Eds). *pp*. 599–602. EDIPUCRS, Porto Alegre.

Casselman, J.M. (1983). Age and growth of fish from their calcified structures – techniques and tools. *National Oceanic and Atmospheric Administration Technical Report NMFS* **8**: 1-17.

Casselman, J.M. (1987). Determination of age and growth. In: *The Biology of Fish Growth* (Weatherley, A.H. and Gill, H.S., Eds). *pp*. 209-242. Academic Press, New York.

Castelnau, F.L. de L. (1872). Contribution to the ichthyology of Australia. *Proceedings of the Zoological Acclimatisation Society of Victoria* **1**: 29-247.

Cavrilets, S., Vose, A., Barluenge, M., Salzburger, W. and Meyer, A. (2007). Case studies and mathematical models of ecological speciation. 1. Cichlids in a crater lake. *Molecular Ecology* **16**: 2893-2909.

Cena, C.J., Morgan, G.E., Malette, M.D. and Heath, D.D. (2006). Inbreeding, outbreeding and environmental effects on genetic diversity in 46 walleye (*Sander vitreus*) populations. *Molecular Ecology* **15**: 303-320.

Cerrato, R.M. (1990). Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences* **47**: 1416-1426.

Chang, W.Y.B. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **39**: 1208-1210.

Chao, N.L. (1978). A basis for classifying western Atlantic Sciaenidae (Teleostei: Perciformes). NOAA Technical Report Circular **415**.

Chao, N.L. (1986). A synopsis on zoogeography of the Sciaenidae. In: *Indo-Pacific Fish Biology. Proceedings of the Second International Conference on Indo-Pacific Fishes*. (Uyeno, T. Arai, R., Taniuchi, T. and Matsuura, K., Eds). *pp*. 570-589. The Ichthyological Society of Japan, Tokyo.

Chao, N.L. and Musick, J.A. (1977). Life history, feeding habits and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. *Fishery Bulletin* **75**: 657-702.

Chaplin, J.A., Baudains, G.A., Gill, H.S. McCulloch, R. and Potter I.C. (1998). Are assemblages of black bream (*Acanthopagrus butcheri*) in different estuaries genetically distinct? *International Journal of Salt Lake Research* **6**: 303-321.

Chapman, D.M., Geary, M., Roy, P.S. and Thom, B.G. (1982). *Coastal Evolution and Coastal Erosion in New South Wales.* Coastal Council of New South Wales, Sydney.

Chen, I.-S., Hsu, C.-H., Hui, C.-F., Shao, K.-T., Miller, P.J. and Fang, L.-S. (1998). Sequence length and variation in the mitochondrial control region of two freshwater gobiid fishes belonging to *Rhinogobius* (Teleostei: Gobioidei). *Journal of Fish Biology* **53**: 179-191.

Choat, J.H., Davies, C.R., Ackerman, J.L. and Mapstone, B.D. (2006). Age structure and growth in a large teleost, *Cheilinus undulatus*, with a review of size distribution in labrid fishes. *Marine Ecology Progress Series* **318**: 237-246.

Chilton, D.E. and Beamish, R.J. (1982). Age determination methods for fishes studied by the Groundfish Program at the Pacific Biological Station. *Canadian Special Publication of Fisheries and Aquatic Sciences* **60**: 1-102.

Christensen, V., Guénette, S., Heymans, J.J., Walters, C.J., Watson, R., Zeller, D. and Pauly, D. (2003). Hundred-year decline of North Atlantic predatory fishes. *Fish and Fisheries* **4**: 1-24.

Chrystal, P. (1983). *The ecology of benthic teleosts in offshore regions of the Swan-Avon Estuary*. Unpublished Honours Thesis. Murdoch University, Perth.

Chu, Y.T., Lo, Y.L. and Wu, H.L. (1963). *A study on the classification of sciaenoid fishes of China, with description of new genera and species*. Science and Technology Press, Shanghai.

Cisneros-Mata, M.A., Montemayor-López, G. and Román-Rodríguez, M.J. (1995). Life history and conservation of *Totoaba macdonaldi*. *Conservation Biology* **9**: 806-814.

Clark, D.L., Leis, J.M., Hay, A.C. and Trnski, T. (2005). Swimming ontogeny of larvae of four temperate marine fishes. *Marine Ecology Progress Series* **292**: 287-300.

Clarke, K.R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**: 117–143.

Clarke, K.R. and Warwick, R.M. (2001). *Change in marine communities: an approach to statistical analyses and interpretation. 2nd edition*. Primer-E Ltd., Plymouth.

Clement, M., Posada, D. and Crandall, K.A. (2000). TCS: a computer program to estimate gene genealogies. *Molecular Ecology* **9**: 1657-1659.

Cliff, G. and Dudley, S.F.J. (1991). Sharks caught in the protective gill nets off Natal, South Africa. 5. The Java shark *Carcharhinus amboinensis* (Muller and Henle). *South African Journal of Marine Science* **11**: 443-453.

Cliff, G., Dudley, S.F.J. and Davis, B. (1989). Sharks caught in the protective gill nets off Natal, South Africa. 2. The great white shark *Carcharodon carcharias* (Linnaeus). *South African Journal of Marine Science* **8**: 131-144.

Coghlan, S. (2000). Guide to Albany beach fishing. *Western Angler*. April-May. *pp.* 56-60.

Coghlan, S. (2007). Spawning aggregation conundrum. *Western Angler*. August-September. *pp.* 9-11.

Colborn, J., Crabtree, R.E., Shaklee, J.B., Pfeiler, E., Bowen, B.W. (2001). The evolutionary enigma of bonefishes (*Albula* spp.): cryptic species and ancient separations in a globally distributed shorefish. *Evolution* **55**: 807–820.

Coleman, F.C., Figueira, W.F., Ueland, J.S. and Crowder, L.B. (2004). The impact of United States recreational fisheries on marine fish populations. *Science* **305**: 1958-1960.

Collins, M.R., Callahan, B.M. and Post, W.C. (2001). *Spawning Aggregations of Recreationally Important Sciaenid Species in the Savannah Harbour: Spotted Seatrout* Cynoscion nebulosus*, Red Drum* Sciaenops ocellatus*, Weakfish* Cynoscion regalis*, and Black Drum* Pogonias cromis. Final Report to Georgia Ports Authority. South Carolina Department of Natural Resources. Marine Resources Institute, Charleston.

Commonwealth of Australia (2006). *A Guide to the Integrated Marine and Coastal Regionalisation of Australia Version 4.0*. Department of the Environment and Heritage, Canberra.

Connaughton, M.A. and Taylor, M.H. (1995). Seasonal and daily cycles in sound production associated with spawning in the weakfish, *Cynoscion regalis*. *Environmental Biology of Fishes* **42**: 233-240.

Conover, D.O., Brown, J.J. and Ehtisham, A. (1997). Countergradient variation in growth of young striped bass (*Morone saxatilis*) from different latitudes. *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 2401-2409.

Conover, D.O. (1992). Seasonality and the scheduling of life history at different latitudes. *Journal of Fish Biology* **41**: 161-178.

Cooke, S.J. and Cowx, I.G. (2006). Contrasting recreational and commercial fishing: searching for common issues to promote unified conservation of fisheries resources and aquatic environments. *Biological Conservation* **128**: 93-108.

Coulson, P.G., Hesp, A., Potter, I.C. and Hall, N.G. (2005). Comparisons between the biology of two co-occurring species of whiting (Sillaginidae) in a large marine embayment. *Environmental Biology of Fishes* **73**: 125-139.

Courchamp, F., Angulo, E., Rivalan, P., Hall, R.J., Signoret, L., Bull, L. and Meinard, Y. (2006). Rarity value and species extinction: The anthropogenic Allee effect. *PloS Biology* **4**: e415.

Cowan Jr., J.H. and Birdsong, R.S. (1985). Seasonal occurrence of larval and juvenile fishes in a Virginia Atlantic coast estuary with emphasis on drums (Family Sciaenidae). *Estuaries* **8**: 48-59.

Cruz, A. and Lombarte, A. (2004). Otolith size and its relationship with colour patterns and sound production. *Journal of Fish Biology* **65**: 1512-1525.

Cusack, R. (2004). *Hooked for Life*. Western Angler Publishing. Perth.

Cusack, R. and Roennfeldt, M. (2002). *Fishing the Wild West*. Pk Print, Perth.

Cyrus, D.P. and Blaber, S.J.M. (1987a). The influence of turbidity on juvenile marine fishes in estuaries. Part 1, Field studies. *Journal of Experimental Marine Biology and Ecology* **109**: 53-70.

Cyrus, D.P. and Blaber, S.J.M. (1987b). The influence of turbidity on juvenile marine fishes in estuaries. Part 2, Laboratory studies. *Journal of Experimental Marine Biology and Ecology* **109**: 71-91.

D'Adamo, N., Simpson, C., Mills, D., Imberger, J. and McComb, A. (1992). The influence of stratification on the ecological response of two Western Australian embayments to nutrient enrichment. *Science of the Total Environment* (Supplement 1992): 829-850.

Dando, P.R. (1984). Reproduction in estuarine fishes. In: *Fish Reproduction: Strategies and Tactics* (Potts, G.W., Wooten, R.J., Eds). *pp.* 155-170. Academic Press, London.

Darovec, J. E. 1983. Sciaenid fishes (Osteichthyes: Perciformes) of western peninsular, Florida. *Memoirs of the Hourglass Cruises* **6**: 1-73.

de Oliviera Santos, M.C.S., Rosso, R.A., Dos Santos, S.H., Lucato, B. and Bassoi, M. (2002). Insights on small cetacean feeding habits in south-eastern Brazil. *Aquatic Mammals* **28**: 38-45.

Department of Environmental Protection (1996). *Southern Metropolitan Coastal Waters Study 1991-1994: Final Report*. Department of Environmental Protection, Perth.

Dulvy, N.K., Sadovy, Y. and Reynolds, J.D. (2003). Extinction vulnerability in marine populations. *Fish and Fisheries* **4**: 25-64.

Ebach, M.C. and Holdrege, C. (2005). DNA barcoding is no substitute for taxonomy. *Nature* **434**: 697.

Edgar, G.J. (2000). *Australian Marine Life: the plants and animals of temperate waters.* Reed New Holland, Sydney.

Excoffier, L., Laval, G. and Schneider, S. (2005). Arlequin version 3.0: an integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online* **1**: 47-50.

Excoffier, L., Smouse, P.E. and Quattro, J.M. (1992). Analysis of molecular variance inferred from metric distances among DNA haplotypes: applications to human mitochondrial DNA restriction data. *Genetics* **131**: 479-491.

Fairclough, D.V., Dimmlich, W.F. and Potter, I.C. (2000). Length and age compositions and growth rates of the australian herring *Arripis Georgiana* in different regions. *Marine and Freshwater Research* **51**: 631-640.

Farmer, B.M. (2003). *Biology of the mulloway* Argyrosomus japonicus *in Western Australia.* Unpublished Honours Thesis. Murdoch University, Perth.

Farmer, B.M., French, D.J.W., Potter, I.C., Hesp, S.A. and Hall, N.G. (2005). *Determination of the biological parameters for managing the fisheries for Mulloway and Silver Trevally in Western Australia*. FRDC Final Report for Project No. 2002/004. Fisheries Research and Development Corporation, Canberra.

Fennessey, S.T. (2000). Aspects of the biology of four species of Sciaenidae from the east coast of South Africa. *Estuarine, Coastal and Shelf Science* **50**: 259-269.

Ferguson, G. and Ward, T. (2003). *Mulloway* (Argyrosomus japonicus) *Fishery*. Fishery Assessment Report to PIRSA Fisheries. SARDI Aquatic Sciences Publication No. RD03/0040. South Australian Research and Development Institute, West Beach.

Ferraro, S.P. (1980). Daily time of spawning of 12 fishes in the Peconic Bays, New York. *Fishery Bulletin* **78**: 455-464.

Fey, D.P. (2006). The effect of temperature and somatic growth on otolith growth: the discrepancy between two clupeid species from a similar environment. *Journal of Fish Biology* **69**: 794-806.

Flanagan and Hendrickson, (1976). Observations on the commercial fishery and reproductive biology of the totoaba, *Cynoscion macdonaldi*, in the northern Gulf of California. *Fishery Bulletin* **74**: 531-544.

Fletcher, W.J. and Head, F. (Eds) (2006). *State of the Fisheries Report 2005/2006*. Department of Fisheries, Perth.

Folkvord, A., Johannessen, A. and Moksness, E. (2004). Temperature dependent otolith growth in herring (*Clupea harengus* L.) larvae. *Sarsia* **89**: 297-310.

Ford, M.J. (2002). Applications of selective neutrality tests to molecular ecology. *Molecular Ecology* **11**: 1245-1262.

Frankham, R. (1995). Conservation genetics. *Annual Review of Genetics* **29**: 305-327.

Froese, R. and Pauly, D. (Eds) (2007). *FishBase. World Wide Web electronic publication*. www.fishbase.org, version (01/2007).

Froukh, T. and Kochzius, M. (2007). Genetic population structure of the endemic fourline wrasse (*Larabicus quadrilineatus*) suggests limited larval dispersal in the Red Sea. *Molecular Ecology* **16**: 1359-1367.

Fu, Y.-X. (1997). Statistical test of neutrality of mutations against population growth, hitchhiking and background selection. *Genetics* **147**: 915-925.

Fu, Y.-X. and Li, W.-H. (1993). Statistical tests of neutrality of mutations. *Genetics* **133**: 693-709.

Gannon, D.P. and Waples, D.M. (2004). Diets of coastal bottlenose dolphins from the U.S. mid-Atlantic coast differ by habitat. *Marine Mammal Science* **20**: 527-545.

Garber, A.F., Tringali, M.D. and Stuck, K.C. (2004). Population structure and variation in Red Snapper (*Lutjanus campechanus*) from the Gulf of Mexico and Atlantic coast of Florida as determined from mitochondrial DNA control region sequence. *Marine Biotechnology* **6**: 175-185.

Gartside, D.F., Harrison, B. and Ryan, B.L. (1999). An evaluation of the use of fishing club records in the management of marine recreational fisheries. *Fisheries Research* **41**: 47-61.

Gaughan, D.J., Neira, F.J., Beckley, L.E. and Potter, I.C. (1990). Composition, seasonality and distribution of the ichthyoplankton in the lower Swan River Estuary, south-western Australia. *Australian Journal of Marine and Freshwater Research* **41**: 529-543.

Gauldie, R.W. (1988). Function, form and time-keeping properties of fish otoliths. *Comparative Biochemistry and Physiology* **91A**: 395-402.

Geffen, A.J. and Nash, R.D.M. (1995). Periodicity of otolith check formation in the juvenile plaice *Pleuronectes platessa*. In: *Recent Developments in Fish Otolith Research* (secor, D.J., Dean, J.M. and Campana, S.E., Eds). *pp*. 65-73. University of South Carolina Press, Columbia.

Gersbach, G.H., Pattiaratchi, C., Ivey, G.N. and Cresswell, G.R. (1999).Upwelling on the south-west coast of Australia – source of the Capes Current? *Continental Shelf Research* **19**: 363-400.

Gillanders, B.M. (1995). Reproductive biology of the protogynous hermaphrodite *Achoerodus viridis* (Labridae) from south-eastern Australia. *Marine and Freshwater Research* **46**: 999-1008.

Godfrey, J.S. and Ridgway, K.R. (1985). The large-scale environment of the poleward-flowing Leeuwin Current, Western Australia: longshore steric height gradients, wind stresses and geostrophic flow. *Journal of Physical Oceanography* **15**: 481-495.

Gold, J.R. and Richardson, L.R. (1994). Genetic distinctness of red drum (*Sciaenops ocellatus*) from Mosquito Lagoon, eastern Florida. *Fishery Bulletin* **92**: 58-66.

Gold, J.R. and Turner, T.F. (2002). Population structure of red drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico, as inferred from variation in nuclear-encoded microsatellites. *Marine Biology* **140**: 249-265.

Gold, J.R., Burridge, C.P. and Turner, T.F. (2001). A modified stepping-stone model of population structure in red drum, *Sciaenops ocellatus* (Sciaenidae), from the northern Gulf of Mexico. *Genetica* **111**: 305-317.

Gold, J.R., Richardson, L.R. and Turner, T.F. (1999). Temporal stability and spatial divergence of mitochondrial DNA haplotype frequencies in red drum (*Sciaenops ocellatus*). From coastal regions of the western Atlantic Ocean and Gulf of Mexico. *Marine Biology* **133**: 593-602.

Gold, J.R., Richardson, L.R., Furman, C. and King, T.L. (1993). Mitochondrial DNA differentiation and population structure in red drum (*Sciaenops ocellatus*) from the Gulf of Mexico and Atlantic Ocean. *Marine Biology* **116**: 175-185.

Gommon, M.F., Glover, J.C.M. and Kuiter, R.H. (Eds) (1994). *The Fishes of Australia's South Coast*. State Print. Adelaide.

Goudet, J. (1996). FSTAT (Version 1.2): A computer program to calculate *F*-statistics. *Journal of Heredity* **86**: 485-486.

Gray, C.A. (1995). *The influences of sewerage plumes and oceanography on assemblages of larval fishes*. Unpublished PhD Thesis. The University of Sydney, Sydney.

Gray, C.A. (2002). Management implications of discarding in an estuarine multi-species gill net fishery. *Fisheries Research* **56**: 177-192.

Gray, C.A. and McDonall, V.C. (1993). Distribution and growth of juvenile mulloway, *Argyrosomus hololepidotus* (Pisces: Sciaenidae), in the Hawkesbury River, south-eastern Australia. *Australian Journal of Marine and Freshwater Research* **44**: 401-409.

Gray, C.A. and Miskiewicz, A.G. (2000). Larval fish assemblages in south-east Australian coastal waters: seasonal and spatial structure. *Estuarine, Coastal and Shelf Science* **50**: 549-570.

Gray, C.A., McDonall, V.C. and Reid, D.D. (1990). By-catch from prawn trawling in the Hawkesbury River, New South Wales: species composition, distribution and abundance. *Australian Journal of Marine and Freshwater Research* **41**: 13-26.

Greenwood, P.H., Rosen, D.E., Weitzman, S.H. and Myers, G.S. (1966). Phylogenetic relationships of teleostean fishes, with a provisional classification of living forms. *Bulletin of the American Museum of Natural History* **131**:339-456.

Griffiths, M.H. (1996). Life history of the dusky kob *Argyrosomus japonicus* (Sciaenidae) off the east coast of South Africa. *South African Journal of Marine Science* **17**: 135-154.

Griffiths, M.H. (1997a). Feeding ecology of the South African *Argyrosomus japonicus* (Pisces: Sciaenidae), with emphasis on the eastern Cape surf zone. *South African Journal of Marine Science* **18**: 249-264.

Griffiths, M.H. (1997b). Management of South African dusky kob *Argyrosomus japonicus* (Sciaenidae) based on per-recruit models. *South African Journal of Marine Science* **18**: 213-228.

Griffiths, M.H. and Hecht, T. (1995a). Age and growth of South African dusky kob *Argyrosomus japonicus* (Sciaenidae) based on otoliths. *South African Journal of Marine Science* **16**: 119-128.

Griffiths, M.H. and Hecht, T. (1995b). On the life history of *Atractoscion aequidens*, a migratory sciaenid off the east coast of southern Africa. *Journal of Fish Biology* **47**: 962-985.

Griffiths, M.H. and Heemstra, P.C. (1995). A contribution to the taxonomy of the marine fish genus *Argyrosomus* (Perciformes: Sciaenidae), with descriptions of two new species from southern Africa. *Ichthyological Bulletin of the J.L.B. Smith Institute of Ichthyology* **65**.

Guest, W.C. and Lasswell, J.L. (1978). A note on courtship behaviour and sound production of red drum. *Copeia* **1978**: 337-338.

Gusmão-Pompiani, P., Oliviera, C. and Quagio-Grassiotto, I. (2005). Spermatozoa ultrastructure in Sciaenidae and Polynemidae (Teleostei: Perciformes) with some consideration on Percoidei spermatozoa ultrastructure. *Tissue and Cell* **37**: 177-191.

Gyllensten, U. (1985). The genetic structure of fish: differences in the intraspecific distribution of biochemical genetic variation between marine, anadromous, and freshwater species. *Journal of Fish Biology* **26**: 691-699.

Haedrich, R.L. (1983). Estuarine fishes. In: *Ecosystems of the World (vol. 26). Estuaries and Enclosed Seas* (Ketchum, B.H., Ed.). *pp.* 183-207. Elsevier Scientific, Oxford.

Hair, J. F., Anderson, R. E., Tatham R. L. and Black, W. C. (1992). *Multivariate Data Analysis with Readings*. Macmillan Publishing, New York.

Hall, D.A. (1984). The Coorong: Biology of the major fish species and fluctuations in catch rates 1976-1983. *SAFIC* **8**: 3-16.

Hall, D.A. (1986). *An assessment of the Mulloway (Argyrosomus hololepidotus) fishery in South Australia with particular reference to Coorong Lagoon.* Discussion Paper, Department of Fisheries, South Australia.

Hall, N.G. (1993). Data requirements of multispecies, spatial, and ecosystem models. In: *Population Dynamics for Fisheries Management. Australian Society for Fish Biology Proceedings* (Hancock, D.A., Ed.). *pp.* 108-113. Australian Government Publishing Services, Canberra.

Hara, J.H. and Law, C.Y.M. (1972). Adaptation of the olfactory bulbar response in fish. *Brain Research* **47**: 259-261.

Hauser, L. and Ward, R.D. (1998). Population identification in pelagic fish: the limits of molecular markers. In: *Advances in Molecular Ecology* (Carvalho, G.R., Ed.). *pp*. 191-224. IOS Press, Oxford.

Hecht, T. and Mperdempes, A. (2001). Screening of *Argyrosomus japonicus* (Sciaenidae) and *Pomadasys commersonnii* (Haemulidae) as candidates for aquaculture in South Africa. Aquaculture 2001 Book of Abstracts. World Aquaculture Society, Coronado Springs Resort, Florida.

Heemstra, P. and Heemstra, E. (2004). *Coastal Fishes of Southern Africa*. The National Inquiry Service Centre (NISC) and the South African Institute for Aquatic Biodiversity (SAIAB), Grahamstown.

Helfman, G.S., Collette, B.B. and Facey, D.E. (1997). *The diversity of Fishes*. Blackwell Science, Malden.

Henry, G.W. and Lyle, J.M. (2003). The National Recreational and indigenous fishing survey. Final Report to the Fisheries Research and Development Corporation and the Fisheries Action Program. Project No. 1999/158. NSW Fisheries Final Report Series No. 48. NSW Department of Primary Industries, Cronulla.

Herbert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H. and Hallwachs, W. (2004). Ten species in one: DNA barcoding reveals cryptic species in the Neotropical skipper butterfly *Astraptes fulgerator. Proceedings of the National Academy of Sciences USA* **101**: 14812-14817.

Hesp, S.A., Potter, I.C. and Hall, N.G. (2002). Age and size composition, growth rate, reproductive biology, and habitats of the West Australian dhufish (*Glaucosoma hebraicum*) and their relevance to the management of this species. *Fishery Bulletin* **100**: 214-227.

Hesp, S.A., Hall, N.G. and Potter, I.C. (2004a). Size-related movements of *Rhabdosargus sarba* in three different environments and their influence on estimates of von Bertalanffy growth parameters. *Marine Biology* **144**: 449-462.

Hesp, S.A., Potter, I.C. and Schubert, S.R.M. (2004b). Factors influencing the timing and frequency of spawning and fecundity of the gold-lined seabream (*Rhabdosargus sarba*) (Sparidae) in the lower reaches of an estuary. *Fishery Bulletin* **102**: 648-660.

Hill, B.J. (1990). Keynote address: minimum legal sizes and their use in the management of Australian fisheries. In: *Minimum legal sizes and their use in fisheries management. Australian Society for Fish Biology workshop proceedings* (Hancock, D.A., Ed.). *pp*. 9-50. Australian Government Publishing Services, Canberra.

Hilborn, R., Branch, T.A., Ernst, W., Magnusson, A., Minte-Vera, C.A., Scheuerell, M.D. and Valero, J.L. (2003). State of the world's fisheries. *Annual Review of Environment and Resources* **28**: 359-399.

Hodgkin, E.P. and Clark, R. (1990). Estuaries of the Shire of Albany, an inventory of information on the estuaries and coastal lagoons of south Western Australia. *Estuarine Study Series* **8**. Environmental Protection Authority, Western Australia.

Hodgkin, E.P. and Hesp, P. (1998). Estuaries to salt lakes: Holocene transformation of the estuarine ecosystems of south-western Australia. *Marine and Freshwater Research* **49**: 183-201.

Hoeksema, S.D. (2006). *Characteristics of the ichthyofaunas of four south-western Australian estuaries with varying degrees of environmental degradation*. Unpublished PhD Thesis. Murdoch University, Perth.

Hoeksema, S.D., Chuwen, B.M., Hesp, S.A., Hall, N.G. and Potter, I.C. (2006). *Impact of environmental changes on the fish faunas of Western Australian south-coast estuaries.* FRDC Final Report for Project No. 2002/017. Fisheries Research and Development Corporation.

Hoese, D.F., Bray, D.J., Paxton, J.R. and Allen, G.R. (2006). Fishes. In: *Zoological Catalogue of Australia. Volume 35, Part 2* (Beesley, P.L. and Wells, A., Eds). *pp*. 671-1472. ABRS and CSIRO Publishing, Collingwood.

Holt, C.P. (1978). *The biology of three teleost species in the Swan River Estuary.* Unpublished Honours Thesis. Murdoch University, Perth.

Holt, G.J., Holt, S.A. and Arnold, C.R. (1985). Diel periodicity of spawning in sciaenids. *Marine Ecology Progress Series* **27**: 1-7.

Holt, S.A. (2002). Intra- and inter-day variability in sound production by red drum (*Sciaenops ocellatus*) at a spawning site. *Bioacoustics* **12**: 227-228.

Howland, K.L., Gendon, M., Tonn, W.M. and Tallman, R.F. (2004). Age determination of a long lived coregonid from the Canadian North: comparison of otoliths, fin rays and scales in inconnu (*Stenodus leucichthys*). *Annales Zoologici Fennici* **41**: 205-214.

Hubert, N., Duponchelle, F., Nunez, J., Garcia-Davilla, C., Paugy, D. and Renno, J.F. (2007). Phylogeography of the piranha genera *Serrasalmus* and *Pygocentrus*: implications for the diversification of the Neotropical ichthyofauna. *Molecular Ecology* **16**: 2115-2136.

Huisman, J.M. (2000). *Marine Plants of Australia.* University of Western Australia Press, Perth.

Hunter, J.R. and Macewicz, B.J. (1985). Measurement of spawning frequency in multiple spawning fishes. In: *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fishes: Application to the Northern Anchovy*, Engraulis mordax (Lasker, R., Ed.). NOAA Technical Report, National Marine Fisheries Service **36**: 79-94.

Hunter, J.R.., Lo, N.C.H. and Leong, R.J.H. (1985). Batch fecundity in multiple spawning fishes. In: *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fishes: Application to the Northern Anchovy*, Engraulis mordax (Lasker, R., Ed.). NOAA Technical Report, National Marine Fisheries Service **36**: 67-77.

Hutchings, J.A. (2001). Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 108-121.

Hutchings, K., Griffiths, M.H. and Field, J.G. (2006). Regional variation in the life history of the canary drum *Umbrina canariensis* (Sciaenidae), in South African waters. *Fisheries Research* **77**: 312-325.

Hutchins, J.B. (1990). Fish survey of South Passage, Shark Bay, Western Australia. In: *Research in Shark Bay, Report of the France-Australe Bicentenary Expedition Committee* (Berry, P.F., Bradshaw, S.D. and Wilson, B.R., Eds). *pp.* 263-278. Western Australian Museum, Perth.

Hutchins, J.B. (1991). Dispersal of tropical fishes to temperate seas in the Southern Hemisphere. *Journal of the Royal Society of Western Australia* **74**: 79-84.

Hutchins, B. and Pearce, A.F. (1994). Influence of the Leeuwin Current on recruitment of tropical reef fishes at Rottnest Island, Western Australia. *Bulletin of Marine Science* **54**: 245-255.

Hutchins, B. and Swainston, R. (2002). *Sea Fishes of Southern Australia*. Swainston Publishing, Smithfield.

Hutchinson, C.A., Newbold, J.E., Potter, S.S. and Edgell, M.H. (1974). Maternal inheritance of mammalian mitochondrial DNA. *Nature* **251**: 536-538.

Iguchi, K., Watanabe, K. and Nishida, M. (2005). Validity of fluctuating asymmetry as a gauge of genetic stress in ayu stocks. *Fisheries Science* **71**: 308-313.

Ihssen, P.E., Booke, H.E., Casselman, J.M., McGlade, J.M., Payne, N.R. and Utter, F.M. (1981). Stock Identification: materials and methods. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 1838-1855.

Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Borque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Esles, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J. and Warner, R.R. (2001). Historical overfishing and collapse of coastal ecosystems. *Science* **293**: 629-638.

James, P.S.B.R. (1994). Endangered, vulnerable and rare marine fishes and animals. In: *Threatened Fishes of India* (Proceedings of the National Seminar on Endangered Species) (Dehadrai, P.V., Das, P. and Verma, S.R., Eds). *pp*. 271-295. India Nature Conservators, Muzaffarnagar.

Jennings, S., Kaiser, M.J. and Reynolds, J.D. (2001). *Marine Fisheries Ecology*. Blackwell Science, Carlton.

Johansen, T., Nyhammer, G., Otterlei, E., Naevdal, G. and Brix, O. (1999). Sexual maturation in cod (*Gadus morhua* L.) in relation to strain, temperature, sex, size and haemoglobin type. In: *Reproductive Physiology of Fish, Proceedings of the Sixth International Symposium, July 4-9, 1999, Bergen, Norway. pp.* 343.

Johnson, G.D. (1993). Percomorph phylogeny: progress and problems. *Bulletin of Marine Science* **52**: 3-28.

Johnson, M.S. (2000). Measuring and interpreting genetic structure to minimise the genetic risk of translocations. *Aquaculture Research* **31**: 133-143.

Johnson, M.S., Watts, R.J. and Black, R. (1994). High levels of genetic subdivision in peripherally isolated populations of the atherinid fish *Craterocephalus capreoli* in the Houtman Abrolhos Islands, Western Australia. *Marine Biology* **119**: 179-184.

Johnson, O., Neely, K. and Waples, R. (2004). Lopsided fish in the Snake River Basin – fluctuating asymmetry as a way of assessing impact of hatchery supplementation in Chinook Salmon, *Onchorynchus tshawytscha*. *Environmental Biology of Fishes* **69**: 379-393.

Johnson, W.S., Allen, D.M., Ogburn, M.V. and Stancyk, S.E. (1990). Short-term predation responses of adult bay anchovies *Anchoa mitchilli* to estuarine zooplankton availability. *Marine Ecology Progress Series* **64**: 55-68.

Jonassen, T.M., Imsland, A.K., Fitzgerald, R., Bonga, S.W., Ham, E.V., Naevadal, G. Stefansson, M.O. and Stefansson, S.O. (2000). Geographic variation in growth and food conversion efficiency of juvenile Atlantic halibut related to latitude. *Journal of Fish Biology* **56**: 279-294.

Jones, D.S. (1990). An annotated checklist of marine decapod Crustacea from Shark Bay, Western Australia. In: *Research in Shark Bay, Report of the France-Australe Bicentenary Expedition Committee* (Berry, P.F., Bradshaw, S.D. and Wilson, B.R., Eds). *pp.* 169-208. Western Australian Museum, Perth.

Kai, Y., Sato, T., Nakae, M., Nakobo, T. and Yoshihiko, M. (2004). Genetic divergence between and within two colour morphotypes of *Parapercis sexfasciata* (Perciformes: Pinguipedidae) from Tosa Bay, southern Japan. *Ichthyological Research* **51**: 381-385.

Kailola, P.J., Williams, M.J., Stewart, R.C., Reichelt, R.E., McNee, A. and Grieve, C. (1993). *Australian Fisheries Resources.* Bureau of Resource Sciences, Department of Primary Industries and Energy and the Fisheries Research and Development Corporation.

Kawasaki, T. (1987). *Fisheries Problems in the Yellow and East China Seas.* Environment and Policy Institute East-West Center, Honolulu.

Kennelly, S.J. (1995). The issue of bycatch in Australia's demersal trawl fisheries. *Reviews in Fish Biology and Fisheries* **5**: 213-234.

Kennelly, S.J., Liggins, G.W. and Broadhurst, M.K. (1998). Retained and discarded by-catch from oceanic prawn trawling in New South Wales, Australia. *Fisheries Research* **36**: 217-236.

Kennish, M.J. (1986). *Ecology of Estuaries*. CRC Press, Boca Raton.

Kimura, D.K. (1980). A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* **16**: 111-120.

Kimura, D.K. and Lyons, J.J. (1991). Between-reader bias and variability in the age-determination process. *Fishery Bulletin* **89**: 53-60.

Kimura, D.K., Mandapat, R.R. and Oxford, S.L. (1979). Method, validity, and variability in the age determination of yellowtail rockfish (*Sebastes flavidus*) using otoliths. *Journal of the Fisheries Research Board of Canada* **36**: 377-383.

Kincaid, H.L. (1976). Effects of inbreeding on rainbow trout populations. *Transactions of the American Fisheries Society* **105**: 273-280.

Kincaid, H.L. (1983) Inbreeding in fish populations used for aquaculture. *Aquaculture* **33**: 215-233.

Klopper, A.W. (2005). *Intraspecific genetic variation in the percoid teleosts* Argyrosomus japonicus *(Temminck and Schlegel, 1843) and* Pomadasys commersonnii *(Lacepède, 1801), as inferred from the mitochondrial control region*. Unpublished Masters Thesis. University of Pretoria, Pretoria.

Knutsen, H., Jorde, P.E., Andre, C. and Stenseth, N.C. (2003). Fine-scales geographical population structuring in a highly mobile species: the Atlantic cod. *Molecular Ecology* **12**: 385-394.

Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Paabo, S., Villablanca, F.X. and Wilson, A.C. (1989). Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proceedings of the National Academy of Sciences of the USA* **86**: 6196-6200.

Kozlowski, J. and Wiegert, R.G. (1987). Optimal age and size at maturity in annuals and perennials with determinate growth. *Evolutionary Ecology* **1**: 231-244.

Laevastu, (1965). *Manual of Methods in Fisheries Biology*. FAO, Rome.

Lagardère, J.P. and Mariani, A. (2006). Spawning sounds in meagre *Argyrosomus regius* recorded in the Gironde estuary, France. *Journal of Fish Biology* **69**: 1697-1708.

Lagler, K.F., Bardach, J.E., Miller, R.R. and May Passino, D.R. (1977). *Ichthyology. 2nd Edition*. John Wiley, New York.

Lai, H., Gallucci, V.F., Gunderson, D.R. and Donnelly, R.F. (1996). Age determination in fisheries: methods and applications to stock assessment. In: *Stock assessment: Quantitative Methods and Applications for Small-scale Fisheries* (Ballucci, V.F., Saila, S.B., Gustafson, D.J. and Rothschild, B.J., Eds). *pp*. 82-178. CRC Press, Florida.

Landweber, L.F. and Dobson, A.P. (Eds) (1999). *Genetics and the Extinction of Species: DNA and the Conservation of Biodiversity.* Princeton University Press, New Jersey.

Law, R. (1979). Optimal life histories under age-specific predation. *American Naturalist* **114**: 399-417.

Legeckis, R. and Cresswell, G. (1981). Satellite observations of sea-surface temperature fronts off the coast of western and southern Australia. *Deep Sea Research* **28A**: 297-306.

Leggett, W.C. and Carscadden, J.E. (1978). Latitudinal variation in the reproductive characteristics of American Shad *Alosa sapidissima*: evidence for population specific life history strategies in fish. *Journal of the Fisheries Research Board of Canada* **35**: 1469-1478.

Leica Microsystems Ltd. (2001). *Leica Image Manager 1000. User Maual*. Heerbrug, Germany.

Leis, J.M. and Trnski, T. (2004). Polynemoidea. In: *The Larvae of Indo-Pacific Coastal Fishes*: *An identification guide to marine fish larvae* (Leis, J.M. and Carson-Ewart, B.M., Eds). *pp*. 435-445. Brill, Boston.

Lemm, A.J., Hegge, B.J. and Masselink, G. (1999). Offshore wave climate, Perth (Western Australia), 1994-1996. *Marine and Freshwater Research* **50**: 95-102.

Lenanton, R.C.J. (1977). Aspects of the ecology of fish and commercial crustaceans of the Blackwood River Estuary, Western Australia. *Western Australian Department of Fisheries and Wildlife Report* **19**.

Lenanton, R.C.J. (1982). Alternative non-estuarine nursery habitats for some commercially and recreationally important fish species of south-western Australia. *Australian Journal of Marine and Freshwater Research* **33**: 881-900.

Lenanton, R.C.J. and Hodgkin, E.P. (1985). Life history strategies of fish in some temperate Australian estuaries. In: *Fish Community Ecology in Estuaries and Coastal Lagoons: Towards an Ecosystem Integration* (Yanez-Arancibia, A., Ed.). *pp*. 267-284. DR (R) UNAM Press, Mexico.

Lessa, E.P. (1990). Multidimensional analysis of geographic genetic structure. *Systematic Zoology* **39**: 242-252.

Lester, N.P., Shuter, B.J. and Abrams, P.A. (2004). Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society B* **271**: 1625-1631.

Liggins, G.W. and Kennelly, S.J. (1996). By-catch from prawn trawling in the Clarence River Estuary, New South Wales, Australia. *Fisheries Research* **25**: 347-367.

Liggins, G.W., Kennelly, S.J. and Broadhurst, M.K. (1996). Observer-based survey of by-catch from prawn trawling in Botany Bay and Port Jackson, New South Wales. *Marine and Freshwater Research* **47**: 877-888.

Lin, S.Y. (1939). Fish air bladders of commercial value in China. *The Hong Kong Naturalist* **9**: 108-118.

Lin, S.Y. (1940). Croakers of the South China Sea. *Journal of the Hong Kong Fisheries Research Station* **1**: 243-254.

Lin, K.Z., Twu, Z.Y. and Chen, C.H. (1998). Induced spawning of the post-reared (*Argyrosomus japonicus*). *Aquatic Animal Disease Control* **31**: 4-7.

Logan, B.W. and Cebulski, D.E. (1970). Sedimentary environments of Shark Bay, Western Australia. *Memoirs of the American Association of Petroleum Geologists* **13**: 1-37.

Loneragan, N.R., Potter, I.C., Lenanton, R.C.J. and Caputi, N. (1987). Influence of environmental variables on the fish fauna of the deeper waters of a large Australian estuary. *Marine Biology* **94**: 631-641.

Loneragan, N.R., Potter, I.C. and Lenanton, R.C.J. (1989). Influence of site, season and year on contributions made by marine, estuarine, diadromous and freshwater species to the fish fauna of a temperate Australian estuary. *Marine Biology* **103**: 461-479.

Luckinbill, L.S. and Clare, M.J. (1985). Selection for life span in *Drosophila melanogaster. Heredity* **55**: 9-18.

Luckinbill, L.S. and Clare, M.J. (1986). A density threshold for the expression of longevity in *Drosophila melanogaster. Heredity* **56**: 329-335.

Luczkovich, J.J., Sprague, M.W., Johnson, S.E. and Pullinger, R.C. (1999). Delimiting spawning areas of weakfish *Cynoscion regalis* (family Sciaenidae), in Pamlico Sound, North Carolina using passive acoustic surveys. *Bioaccoustics* **10**: 143-160.

Luczkovich, J.J., Daniel III, H.J., Hutchinson, M., Jenkins, T., Johnson, S.E., Pullinger, R.C. and Sprague, M.W. (2000). Sounds of sex and death in the sea: bottlenose dolphin whistles suppress mating choruses of silver perch. *Bioacoustics* **10**: 323–334.

Lychakov, D.V. & Rebane, Y.T. (2000). Otolith regularities. *Hearing Research* **143**: 83–102.

Lychakov, D.V. & Rebane, Y.T. (2002). Otolith regularities. *Bioacoustics* **12**: 125-128.

Macchi, G.J., Acha, E.M. and Lasta, C.A. (1996). Desove y fecundidad de la corvine rubia (*Micropogonias furnieri*, Dermarest, 1826) en el estuario del Rio de la Plata, Argentina. *Boletin del Instituto Espanol de Oceanografia* **12**: 99-113.

Macchi, G.J., Acha, E.M. and Lasta, C.A. (2002). Reproduction of black drum (*Pogonias cromis*) in the Río de la Plata estuary, Argentina. *Fisheries Research* **59**: 83-92.

Macchi, G.J., Acha, E.M. and Militelli, M.I. (2003). Seasonal egg production of the whitemouth croaker (*Micropogonias furnieri*) in the Río de la Plata estuary, Argentina-Uruguay. *Fishery Bulletin* **101**: 332-342.

Mace, G.M. and Hudson, E.J. (1999). Attitudes towards sustainability and extinction. *Conservation Biology* **13**: 242-246.

MacDonald, C.M. (1980). *Population structure, biochemical adaptation and systematics in temperate marine fishes of the genera* Arripis *and* Chrysophrys *(Pisces: Perciformes)*. Unpublished PhD Thesis. Australian National University, Canberra.

Mackie, M. and Lewis, P. (2001). Assessment of gonad staging systems and other methods used in the study of the reproductive biology narrow-barred Spanish mackerel, *Scomberomorus commersoni*, in Western Australia. Fisheries Research Report No. 136. Western Australian Department of Fisheries, North Beach.

Malling, C. and Grönwall, K.A. (1909). En Fauna i Bornholms Lias. Meddelelser fra Dansk Geologisk Forening, Copenhagen **15**: 271-312.

Malseed, B.E. and Sumner, N.R. (2001). *A 12-month survey of recreational fishing in the Swan Estuary basin of Western Australia during 1998-99.* Fisheries Research Report No. 126. Western Australian Department of Fisheries, Perth.

Mana, R.R. and Kawamura, G. (2002). A comparative study on morphological differences in the olfactory system of red sea bream (*Pagrus major*) and black sea bream (*Acanthopagrus schlegeli*) from wild and cultured stocks. *Aquaculture* **209**: 285-306.

Mann-Lang, J.B. and Buxton, C.D. (1996). Growth characteristics in the otoliths of selected South African sparid fish. *South African Journal of Marine Science* **17**: 205-216.

Marais, J.F.K. (1981). Seasonal abundance, distribution, and catch per unit effort using gill nets, of fishes in the Sundays Estuary. *South African Journal of Zoology* **16**: 144-150.

Marais, J.F.K. (1983a). Seasonal abundance, distribution and catch per unit effort of fishes in the Krom Estuary, South Africa. *South African Journal of Zoology* **18**: 96-102.

Marais, J.F.K. (1983b). Fish abundance and distribution in the Gamtoos Estuary with notes on the effect of floods. *South African Journal of Zoology* **18**: 103-109.

Marais, J.F.K. and Baird, D. (1980). Seasonal abundance, distribution and catch per unit effort of fishes in the Swartkops Estuary. *South African Journal of Zoology* **15**: 66-71.

Marsh, (1990). Hermatypic corals of Shark Bay, Western Australia. In: *Research in Shark Bay, Report of the France-Australe Bicentenary Expedition Committee* (Berry, P.F., Bradshaw, S.D. and Wilson, B.R., Eds). *pp.* 115-128. Western Australian Museum, Perth.

Martínez-Palacios, C.A., Chávez-Sosa, J.C., Santoyo-Guzmán, C.O., Campos-Mendoza1, A., Martinez-Chavez, C.C. and Ross, L.G. (2007). The effect of photoperiod on the reproduction of *Chirostoma estor estor* Jordan 1879 from Lago de Pátzcuaro, Mexico. *Journal of Applied Ichthyology* **23**: 621-623.

Masselink, G. and Pattiaratchi, C.B. (2001). Seasonal changes in beach morphology along the sheltered coastline of Perth, Western Australia. *Marine Geology* **172**: 243-263.

Massou, A.M., Panfili, J., Le Bail, P.-Y., Lae, R., Mikolasek, O., Fontenelle, G. and Baroiller, J.F. (2004). Evidence of perturbations induced by reproduction on somatic growth and microincrement deposition in *Oreochromis nilocticus* otoliths. *Journal of Fish Biology* **64**: 380-398.

Maxwell, J.G.R. and Cresswell, G.R. (1981). Dispersal of tropical marine fauna to the Great Australian Bight by the Leeuwin Current. *Australian Journal of Marine and Freshwater Research* **32**: 493-500.

May, B. and Grewe, P.M. (1993). Fate of maternal mtDNA following ^{60}Co inactivation of maternal nuclear DNA in unfertilised salmonid eggs. *Genome* **36**: 725-730.

McAllister, D.E. (1968). Evolution of branchiostegals and classification of teleostome fishes. *National Museum of Canada Bulletin* **221**.

McBride, R.S., Fahay, M.P. and Able, K.W. (2002). Larval and settlement periods of the northern searobin (*Prionotus carolinus*) and the striped searobin (*P. evolans*). *Fishery Bulletin* **100**: 63-73.

McCauley, R. and Simpendorfer, C. (2003). *Catch composition of the Western Australia temperate demersal gillnet and demersal longline fisheries, 1994 to 1999.* Fisheries Research Report No. 146. Department of Fisheries, Western Australia.

McClusky, D.S. and Elliott, M. (2004). *The Estuarine Ecosystem. Ecology, Threats, and Management*. Oxford University Press, New York.

McMillan, W.O. and Palumbi, S.R. (1997). Rapid rate of control region evolution in Pacific butterflyfishes (Chaetodontidae). *Journal of Molecular Evolution* **45**: 473-484.

McPhee, D.P., Leadbitter, D., Skilleter, G.A. (2002). Swallowing the bait: is recreational fishing ecologically sustainable? *Pacific Conservation Biology* **8**: 40-51.

McPherson, G.R. (1992). Assessing macroscopic and histological staging of yellowfin tuna ovaries in the north-western Coral Sea. Information Series of the Department of Primary Industries, Queensland, Q192021.

Meggs, L.B., Austin, C.M. and Coutin, P.C. (2003). Low allozyme variation in snapper, *Pagrus auratus*, in Victoria, Australia. *Fisheries Management and Ecology* **10**: 155-162.

Meirmans, P.G. (2006). Using the AMOVA framework to estimate a standardised genetic differentiation measure. *Evolution* **60**: 2399-2402.

Meyer, A., Kocher, T.D., Basasibwaki, P. and Wilson, A.C. (1990). Monophyletic origin of Lake Victoria cichlid fishes suggested by mitochondrial DNA sequences. *Nature* **347**: 550-553.

Michod, R.E. (1979). Evolution of life histories in response to age-specific mortality factors. *American Naturalist* **113**: 531-550.

Migaud, H., Mandiki, R., Gardeur, J.N., Kestemont, P., Bromage, N.R. and Fontaine, P. (2003). Influence of photoperiod regimes on the Eurasian perch gonadogenesis and spawning. *Fish Physiology and Biochemistry* **28**: 395-397.

Migaud, H., Fontaine, P., Kestemont, P., Wang, N. and Brun-Bellut, J. (2004). Influence of photoperiod on the onset of gonadogenesis in Eurasian perch *Perca fluviatilis*. *Aquaculture* **241**: 561-574.

Millar, R.B. and Meyer, R. (2000). Bayesian state-space modeling of age-structured data: fitting a model is just the beginning. *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 43-50.

Millitelli, M.I. and Macchi, G.J. (2000). Reproduccion de la pescadilla real, *Macrodon ancylodon*, del area rioplatense. IV. Fornadas Nacionales de Ciencias del Mar 11-15 de Septiembre, Peurto Madryn, Argetina.

Mina, M.V. (1968). A note on a problem in the visual qualitative evaluation of otolith zones. *ICES Journal of Marine Science* **40**: 211-219.

Miskiewicz, A.G. (1987). *Taxonomy and ecology of fish larvae in Lake Macquarie and New South Wales coastal waters*. Unpublished PhD Thesis. The University of New South Wales, Sydney.

Mok, H.K. and Gilmore, R.G. (1983). Analysis of sound production in estuarine aggregations of *Pogonias cromis, Bairdiella chrysoura* and *Cynoscion nebulosus* (Sciaenidae). *Bulletin of the Institute of Zoology, Academia Sinica* **22**: 157-186.

Monsch, K.A. (1998). Miocene fish faunas from the northwestern Amazonian basin (Columbia, Peru, Brazil) with evidence of marine incursions. *Palaeogeography, Palaeoclimatology, Palaeoecology* **143**: 31-50.

Morales-Nin, B. and Ralston, S. (1990). Age and growth of *Lutjanus kasmira* (Forskal) in Hawaiian waters. *Journal of Fish Biology* **36**: 191-203.

Morales-Nin, B., Tores, G.J., Lombarte, A. and Recasens, L. (1998). Otolith growth and age estimation in the European hake. *Journal of Fish Biology* **53**: 1155-1168.

Morgan, S.G. (1990). Impact of planktivorous fishes on dispersal, hatching and morphology of estuarine crab larvae. *Ecology* **71**: 1639-1652.

Moritz, C., Dowling, T.E. and Brown, W.M. (1987). Evolution of animal mitochondrial DNA: relevance for population biology and systematics. *Annual Review of Ecology and Systematics* **18**: 269-292.

Mtakovčić, M. and Haley, L.E. (1979). Inbreeding depression in the zebra fish *Brachydanio rerio* (Hamilton Buchanan). *Journal of Fish Biology* **15**: 323-327.

Muhling, B. (2006). *Larval fish assemblages in coastal, shelf and offshore waters of south-western Australia.* Unpublished PhD Thesis. Murdoch University, Perth.

Murphy, M.D. and Taylor, R.G. (1990). Reproduction, growth, and mortality of red drum, *Sciaenops ocellatus*

Musick, J.A. (1999). Criteria to define extinction risk in marine fishes. *Fisheries* **24**: 6-14.

Nachman, M.W. (1998). Deleterious mutations in animal mitochondrial DNA. *Genetica* **103**: 61-69.

Nahas, E.L., Pattiaratchi, C.B. and Ivery, G.N. (2005). Processes controlling the position of frontal systems in Shark Bay, Western Australia. *Estuarine, Coastal and Shelf Science* **65**: 463-474.

Nei, M. (1987). *Molecular Evolutionary Genetics*. Columbia University Press, New York.

Nelson, J.S. (1984). *Fishes of the world* (2nd Edition). John Wiley, New York.

Nelson, J.S. (2006). *Fishes of the World* (4th Edition). John Wiley, New Jersey.

Nolf, D. (1976a). Les otolithes des téléostéens néogénes de Trinidad. Ecologae Geologicae Helvetiae **69**: 703-742.

Nolf, D. (1976b). Les otolithes des téléostéens de L'oligo-Miocéne belge. *Annales de la Societe royale Zoologique de Belgie* **106**: 3-119.

Nurthen, R.K., Cameron, R. and Briscoe, D.A. (1992). Population genetics of tailor *Pomatomus saltatrix* (Linnaeus) (Pisces: Pomatomidae), in Australia. *Australian Journal of Marine and Freshwater Research* **43**: 1481-1486.

Palumbi, S.R. (1992). Marine speciation on a small planet. *Trends in Ecology and Evolution* **7**: 114-118.

Palumbi, S.R. (1994). Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics* **25**: 547-572.

Panella, G. (1980). Growth patterns in fish sagittae. In: *Skeletal Growth of Aquatic Organisms* (Rhoads, D.C. and Lutz, R.A., Eds). *pp*. 519-560. Plenum Press, New York.

Parsons, M.J.G., McCauley, R.D. and Mackie, M.C. (2006). Spawning sounds of the mulloway (*Argyrosomus japonicus*). *Australasian Acoustical Society, conference proceedings, Christchurch, New Zealand, November 19th-22nd, 2006*.

Parsons, M.J.G., McCauley, R.D., Mackie, M.C., Lewis, P., Gill, H. and Gaughan, D. (in prep.). *Management and monitoring of fish spawning aggregations within the west coast bioregion of Western Australia.* Fisheries Research and Development Corporation and the Western Australian Department of Fisheries.

Partridge, G.J., Sarre, G.A., Hall, N.G., Jenkins, G.I., Chaplin, J.A. and Potter, I.C. (2003). Comparisons between the growth of *Acanthopagrus butcheri* cultured from two estuarine populations that are reproductively isolated and differ markedly in growth rate. *Aquaculture* **231**: 51-58.

Paterson, A.W. and Whitfield, A.K. (2000a). Do shallow-water habitats function as refugia for juvenile fishes? *Estuarine, Coastal and Shelf Science* **51**: 359-364.

Paterson, A.W. and Whitfield, A.K. (2000b). The ichthyofauna associated with an intertidal creek and adjacent eelgrass beds in the Kariega Estuary, South Africa. *Environmental Biology of Fishes* **58**: 145-156.

Pauly, D., Alder, J., Bennett, E., Christensen, V., Tyedmers, P., Watson, R. (2003). The future for fisheries. *Science* **302**: 1359–1361.

Pauly, D., Christensen, V., Guénette, S., Pitcher, T., Rashid Sumalia, U., Walters, C.J., Watson, R. and Zeller, D. (2002). Towards sustainability in world fisheries. *Nature* **418**: 689-695.

Pawson, M.G. and Jennings, S. (1996). A critique of methods for stock identification in marine capture fisheries. *Fisheries Research* **25**: 203-217.

Paxton, J.R. (2000). Fish otoliths: do sizes correlate with taxonomic group, habitat and/or luminescence? *Philosophical Transactions of the Royal Society of London* **355**: 1299–1303.

Payan, P., Kossmann, H., Watrin, A., Mayer-Gostan, N. and Bouef, G. (1997). Ionic composition of endolymph in teleosts: origin and importance of endolymph alkalinity. *Journal of Experimental Biology* **200**: 1905-1912.

Pearce, A.F. and Pattiaratchi, C. (1999). The Capes Current: a summer countercurrent flowing past Cape Leeuwin and Cape Naturaliste, Western Australia. *Continental Shelf Research* **19**: 401-420.

Pearce, J.M. (2006). Minding the gap: frequency of indels in mtDNA control region sequence data and influence on population genetic analyses. *Molecular Ecology* **15**: 333-341.

Pember, M.B. (1999). *Characteristics of the fish fauna of nearshore sandy habitats in Shark Bay, Western Australia*. Unpublished Honours Thesis. Murdoch University, Perth.

Penn, J.W. (1977). Trawl caught fish and crustaceans from Cockburn Sound. *Western Australian Department of Fisheries and Wildlife Report* **20**.

Penn, J.W. (Ed.) (2003). *State of the Fisheries Report 2002/2003*. Department of Fisheries, Western Australia.

Peters, K.M. and McMichael, R.H. (1990). Early life history of the black drum *Pogonias cromis* (Pisces: Sciaenidae) in Tampa Bay, Florida. *Northeast Gulf Science* **11**: 39-58.

Phelan, M.J. (2002). *Fishery biology and management of the black jewfish Protonibea diacanthus (Sciaenidae) aggregations near Injinoo Community, far northern Cape York*. FRDC Final Report 98/135.

Phelps, S.R., LeClair, L.L., Young, S. and Blankenship, H.L. (1994). Genetic diversity patterns of chum salmon in the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences* **51**(Supplement 1): 65-83.

Pitcher, T.J., Watson, R., Courtney, A.M. and Pauly, D. (1998). Assessment of Hong Kong's inshore fishery resources. *Fisheries Centre Research Reports* **6**: 1-168.

Planes, S., Galzin, R., Bonhomme, F. (1996). A genetic metapopulation model for reef fishes in oceanic islands: the case of the surgeonfish, *Acanthurus triostegus. Journal of Evolutionary Biology* **9**: 103-117.

Planes, S., Parroni, M. and Chauvet, C. (1998). Evidence of limited gene flow in three species of coral reef fishes in the lagoon of New Caledonia. *Marine Biology* **130**: 361-368.

Post, J.R., Sullivan, M., Cox, S., Lester, N.P., Walters, C.J., Parkinson, E.A., Paul, A.J., Jackson, L. and Shuter, B.J. (2002). Canada's recreational fishery: the invisible collapse? *Fisheries* **27**: 6–17.

Potter, I.C. and Hyndes, G.A. (1999). Characteristics of the ichthyofaunas of southwestern Australian estuaries, including comparisons with holarctic estuaries and estuaries elsewhere in temperate Australia: A review. *Australian Journal of Ecology* **24**: 395-421.

Potter, I.C., Loneragan, N.R., Lenanton, R.C.J., Chrystal, P.J. and Grant, C.J. (1983). Abundance, distribution and age structure of fish populations in a Western Australian estuary. *Journal of Zoology (London)* **200**: 21-50.

Potter, I.C., Beckley, L.E., Whitfield, A.K. and Lenanton, R.C.J. (1990). Comparisons between the roles played by estuaries in the life cycles of fishes in temperate Western Australia and southern Africa. *Environmental Biology of Fishes* **28**: 143-178.

Potter, I.C., Ivantsoff, W., Cameron, R. and Minnard, J. (1986). Life cycles and distribution of atherinids in the marine and estuarine waters of southern Australia. *Hydrobiologia* **139**: 23-40.

Powles, H., Bradford, M.J., Bradford, R.G., Doubleday, W.G., Innes, S. and Levings, C.D. (2000). Assessing and protecting endangered marine species. *International Council for Exploration of the Seas, Journal of Marine Science* **57**: 669-676.

Quagio-Grassiotto, I., Gameiro, M.C., Schneider, T. Malabarba, L.R. and Oliveira, C. (2003). Spermiogenesis and spermatozoa ultrastructure in five species of the Curimatidae with some considerations on spermatozoal ultrastructure in Characiformes. *Neotropical Ichthyology* **1**: 35-45.

Ramcharitar, J., Higgs, D.M. & Popper, A.N. (2001). Sciaenid inner ears: a study in diversity. *Brain, Behavior and Evolution* **58**: 152-162.

Ramcharitar, J., Gannon, D.P. and Popper, A.N. (2006). Bioaccoustics of fishes of the family Sciaenidae (Croakers and Drums). *Transactions of the American Fisheries Society* **135**: 1409-1431.

Ramsey, P.R. and Wakeman, J.M. (1987). Population structure of *Sciaenops ocellatus* and *Cynoscion nebulosus* (Pisces: Sciaenidae): Biochemical variation, genetic subdivision and dispersal. *Copeia* **1987**: 682-695.

Rand, D.M. (2001). The units of selection on mitochondrial DNA. *Annual Reviews in Ecology and Systematics* **32**: 415-448.

Rand, D.M. and Kann, L.M. (1998). Mutation and selection at silent and replacement sites in the evolution of animal mitochondrial DNA. *Genetica* **103**: 393-407.

Raymond, M. and Rousset, F. (1995). GENEPOP (version 1.2): Population genetics software for exact tests and ecumenicism. *Journal of Heredity* **86**: 248-249.

Reay, P.J. (1972). The seasonal pattern of otolith growth and its application to back-calculation studies in *Amnodytes tobianus*. *ICES Journal of Marine Science* **34**: 485-504.

Reznick, D.A. and Endler, J.A. (1982). The impact of predation on life history evolution in Trinidadian guppies (*Poecilia reticulate*). *Evolution* **36**: 160-177.

Reznick, D.A.. Bryga, H. and Endler, J.A. (1990). Experimentally induced life-history evolution in a natural population. *Nature* **346**: 357-359.

Rice, W.R. (1989). Analyzing tables of statistical tests. *Evolution* **43**: 223-225.

Richards, L.J., Schnute, J.T. and Hand, C.M. (1990). A multivariate maturity model with a comparative analysis of three lingcod (*Ophiodon elongatus*) stocks. *Canadian Journal of Fisheries and Aquatic Sciences* **47**: 948-959.

Riggert, T.L. (1978). The Swan River Estuary. Development, Management and Preservation. Frank Daniels Pty. Ltd., Perth.

Roberts, C.M. and Hawkins, J.P. (1999). Extinction risk in the sea. *Trends in Ecology and Evolution* **14**: 241-246.

Roff, D.A. (1983). An allocation model of growth and reproduction in fish. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 1395-1404.

Rooker, J.R., Holt, S.A., Soto, M.A. and Holt, G.J. (1998). Post settlement patterns of habitat use by sciaenid fishes in subtropical sea grass meadows. *Estuaries* **21**: 318-327.

Rose, M.R. (1984). Laboratory expression of postponed senescence in *Drosophila melanogaster. Evolution* **38**: 1004-1010.

Ross, G.J.B., Heinsohn, G.E. and Cockcroft, V.G. (1994). Humpback dolphins *Sousa chinensis* (Osbeck 1765), *Sousa plumbea* (G. Cuvier 1829) and *sousa teuszii* (Kukenthal 1892). In: *Handbook of Marine Mammals: the First Book of Dolphins* (Ridgway, S.H. and Harrison, R., Eds). *pp*. 23-42. Academic Press, New York.

Rowell, K., Flessa, K.W., Dettman, D.L. and Román, M. (2005). The importance of Colorado River flow to nursery habitats of the Gulf corvine (*Cynoscion othonopterus*). *Canadian Journal of Fisheries and Aquatic Sciences* **62**: 2874-2885.

Rozas, J., Sánchez-DelBarrio, J. C., Messeguer, X. and Rozas, R. (2003). DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics* **19**: 2496-2497.

Rutherford, E.S. (2002). Fishery Management. In: *Fishery Science. The Unique Contributions of Early Life Stages* (Fuiman, L.A. and Werner, R.G., Eds). *pp*. 206-221. Blackwell Publishing, Oxford.

Sadovy, Y. (1996). Reproduction in reef fishery species. In: *Reef Fisheries* (Polunin, N.V.C. and Roberts, C.M., Eds). *pp.* 15-59. Chapman and Hall, London.

Sadovy, Y. (2001). The threat of fishing to highly fecund fishes. *Journal of Fish Biology* **59**(Suppl. A): 90-108.

Sadovy, Y. and Cheung, W.L. (2003). Near extinction of a highly fecund fish: the one that nearly got away. *Fish and Fisheries* **4**: 86-99.

Sadovy, Y., Kulbicki, M., Labrosse, P., Letourneur, Y., Lokani, P. and Donaldson, T.J. (2003). The humphead wrasse, *Cheilinus undulatus*: synopsis of a threatened and poorly known giant coral reef fish. *Reviews in Fish Biology and Fisheries* **13**: 327-364.

Salini, J., Brewer, D., Farmer, M. and Jones, P. (2001). Lunar periodicity of prawns and by-catch in trawls from the Gulf of Carpentaria, northern Australia. *Marine Biology* **138**: 975-983.

Sampson, D.B. and Al-Jufaily, S.M. (1999). Geographic variation in the maturity and growth schedules of English sole along the U.S. west coast. *Journal of Fish Biology* **54**: 1-17.

Santos, S., Schneider, H. and Sampaio, I. (2003). Genetic differentiation of *Macrodon ancylodon* (Sciaenidae, Perciformes) populations in Atlantic coastal waters of South America as revealed by mtDNA analysis. *Genetics and Molecular Biology* **26**: 151-161.

Santos, S., Hrbek, T., Farias, I.P., Schneider, H. and Sampaio, I. (2006). Population genetic structuring of the king weakfish, *Macrodon ancylodon* (Sciaenidae), in Atlantic coastal waters of South America: deep genetic divergence without morphological change. *Molecular Ecology* **15**: 4361-4373.

Sarre, G.A. and Potter, I.C. (2000). Variation in age compositions and growth rates of *Acanthopagrus butcheri* (Sparidae) among estuaries: some possible contributing factors. *Fishery Bulletin* **98**: 785-799.

Sasaki, K. (1985). *Comparative anatomy and phylogenetic relationships of the family Sciaenidae* (*Teleostei, Perciformes*). Unpublished Masters Thesis, Hokkaido University, Hokkaido.

Sasaki, K. (1989). Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). *Memoirs of the Faculty of Fisheries, Hokkaido University* **35**:1-137.

Sasaki, K. (1992). Two new and two resurrected species of the sciaenid genus *Johnius* (*Johnius*) from the West Pacific. *Gyoruigaki Zasshi* **39**: 1-168.

Sasaki, K. (2000). Sciaenidae. Croakers and drums. In: A Checklist of fishes of the south China Sea (Randall, J.E., and Lim, K.K.P., Eds). *Raffles Bulletin of Zoology* **8**: 569-667.

Saucier, M.H. and Baltz, D.M. (1993). Spawning site selection by spotted seatrout, *Cynoscion nebulosus*, and black drum, *Pogonias cromis*, in Louisiana. *Environmental Biology of Fishes* **36**: 257-272.

Scheiner, S.M. (1993). Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics* **25**: 35-68.

Schlichting, C.D. and Pigliucci, M. (1998). *Phenotypic Evolution: a Reaction Norm Perspective*. Sinauer Associates, Sunderland.

Schluter, D. (1996). Ecological causes of adaptive radiation. *The American Naturalist* **148**(supplement): 40-64.

Schmidt, H.A., Strimmer, K., Vingron, M. and von Haeseler, A. (2002). TREE-PUZZLE: maximum likelihood phylogenetic analysis using quartets and parallel computing. *Bioinformatics* **18**: 502-504.

Schmidt, W. (1968). Vergleichend morphologische Studie uber die Otolithen mariner Knochenflsche. Archiv fur Fischereiwissenschaft 19 (Beiheft 1).

Schnute, J. (1981). A versatile growth model with statistically stable parameters. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 1128-1140.

Schramm Jr, H.L. (1989). Formation of annuli in otoliths of bluegills. *Transactions of the American Fisheries Society* **118**: 546-555.

Schwarzhans, W. (1993). *Piscium Catalogus. Part Otolithi Piscium vol. 1. A comparative morphological treatise of recent and fossil otoliths of the family Sciaenidae (Perciformes).* Verlag Dr. Friedrich Pfeil, Munchen.

Seddon, G. (1972). *Sense of Place.* University of Western Australia Press, Perth.

Seyoum, S., Tringali, M.D. and Bert, T.M. (2000). An analysis of genetic population structure in red drum, *Sciaenops ocellatus*, based on mtDNA control region sequences. *Fishery Bulletin* **98**: 127-138.

Shaklee, J.B. and Currens, K.P. (2003). Genetic stock identification and risk assessment. In: *Population Genetics: Principles and Applications for Fisheries Scientists* (Hallerman, E.M., Ed.). *pp.* 291-328. American Fisheries Society, Bethesda.

Silberschneider, V. and Gray, C.A. (2005). *Arresting the decline of the commercial and recreational fisheries for mulloway* (Argyrosomus japonicus). FRDC Final Report 2002/05. Fisheries Final Report Series No. 82. New South Wales Department of Primary Industries, Cronulla.

Silberschneider, V. and Gray, C.A. (2007). Synopsis of biological, fisheries and aquaculture-related information on mulloway *Argyrosomus japonicus* (Pisces: Sciaenidae), with particular reference to Australia. *Journal of Applied Ichthyology* **24**: 7-17.

Simkiss, K. (1974). Ca metabolism of fish in relation to ageing. In: *The Ageing of Fish* (Bagenal, T.B., Ed.). *pp*. 1-12. Unwin Brothers, London.

Sinque, C. and Muelbert, J.H. (1997). Environment and biota of the Patos Lagoon Estuary: ichthyoplankton. In: *Subtropical convergence Environments: The Coast and Sea in the southwestern Atlantic* (Seeliger, U., Ed.). *pp.* 51-56. Springer-Verlag, Heidelberg.

Slack-Smith, S.M. (1990). The bivalves of Shark Bay, Western Australia. In: *Research in Shark Bay, Report of the France-Australe Bicentenary Expedition Committee* (Berry, P.F., Bradshaw, S.D. and Wilson, B.R., Eds). *pp.* 129-157. Western Australian Museum, Perth.

Smale, M.J. (1985). Aspects of the biology of *Argyrosomus hololepidotus* (and *Atractoscion aequidens* (Osteichthyes: Sciaenidae) in waters of the south-eastern Cape, South Africa. *South African Journal of Marine Science* **3**: 63-75.

Smith, D.C., Fenton, G.E., Robertson, S.G. and Short, S.A. (1995). Age determination and growth of orange roughy (*Hoplostethus atlanticus*): a comparison of annulus counts with radiometric ageing. *Canadian Journal of Fisheries and Aquatic Sciences* **52**: 391-401.

Smith, H.M. (1905). The drumming of the drum-fishes (Sciaenidae). *Science* **22**: 376-378.

Smith, K.A. (2003). Larval distributions of some commercially valuable fish species over the Sydney continental shelf. *Proceedings of the Linnean Society of New South Wales* **124**: 1-11.

Smith, K.A. (2006). Review of fishery resources and status of key fishery stocks in the Swan-Canning Estuary. Fisheries Research Report No. 156. Department of Fisheries, Perth.

Smith, K.A. and Deguara, K. (2003). Formation and annual periodicity of opaque zones in sagittal otoliths of *Mugil cephalus* (Pisces: Muglidae). *Journal of Marine and Freshwater Research* **54**: 57-67.

Smith, K.A., Brown, J. and Lai, E. (2006). South Coast Estuarine Managed Fishery Status Report. In: *State of the Fisheries Report 2005/2006*. *pp*. 196-224. Department of Fisheries, Perth.

Smith, M.A., Woodley, N.E., Janzen, D.H., Hallwachs, W. and Herbert, P.D.N. (2006). DNA barcodes reveal cryptic host-specificity within the presumed polyphagous members of a genus of parasitoid flies (Diptera: Tachinidae). *Proceedings of the National Academy of Sciences of the United States of America* **103**: 3657-3662.

Smith, P.J., Jamieson, A. and Birley, A.J. (1990). Electrophoretic studies and stock concept in marine teleosts. *Conseil Permanent International pour l'Exploration de la Mer* **47**: 231-245.

Smith, T.B. and Skulason, S. (1996). Evolutionary significance of resource polymorphisms in fishes, amphibians and birds. *Annual Review of Ecology and Systematics* **27**: 111-133.

Smith, T.D. (2002). A history of fisheries and their science and management. In: *Handbook of Fish Biology and Fisheries, vol. II* (Hart, P. and Reynolds, J., Eds). *pp*. 61–83. Blackwell Science, Oxford.

SPSS Inc. (2006). Statistical Package for the Social Sciences (SPSS 15.0) for Windows. SPSS Inc, Chicago.

Stearns, S.C. (1983). A natural experiment in life-history evolution: field data on the introduction of mosquitofish (*Gambusia affinis*) to Hawaii. *Evolution* **37**: 601-617.

Steffe, A.S. (1991). *Larval fish distributions within Botany Bay: Implications for estuarine recruitment and management*. Unpublished PhD Thesis. Macquarie University, Sydney.

Steffe, A.S., Murphy, J.J., Chapman, D.J., Tarlinton, B.E., Gordon, G.N.G. and Grinberg, A. (1996). An assessment of the impact of offshore recreational fishing in New South Wales waters on the management of commercial fisheries. Project No. 94/053. New South Wales Fisheries, Cronulla.

Stephens, R. and Imberger, J. (1997). Intertidal motions within the deep basin of the Swan River Estuary. *Journal of Hydraulic Engineering* **123**: 863-873.

Stunz, G.W., Minello, T.J., Levin, P.S. (2002). A comparison of early juvenile red drum densities among various habitat types in Galveston Bay, Texas. *Estuaries* **25**: 76–85.

Sturman, A.P. and Tapper, N.J. (1996). *The Weather and Climate of Australia and New Zealand*. Oxford University Press, Oxford.

Sultan, S.E. and Stearns, S.C. (2005). Environmentally contingent variation: phenotypic plasticity and norms of reaction. In: *Variation* (Hallgrimsson, B. and Hall, B., Eds). *pp*. 303-332. Elsevier Academic Press, Boston.

Suquet, M., Normant, Y., Gaignon, J.L., Quemener, L. and Fauvel, L. (2005). Effect of water temperature on individual reproductive activity of Pollack (*Pollachius pollachius*). *Aquaculture* **243**: 113-120.

Swearer, S.E., Caselle, J.E., Lea, D.W. and Warner, R.R. (1999). Larval retention and recruitment in an island population of a coral reef fish. *Nature* **402**: 799-802.

Tajima, F. (1989). Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* **123**: 585-595.

Takemura, A., Takita, T. and Mizue, K. (1978). Studies on the underwater sound VII: Underwater calls of the Japanese marine drum fishes (Sciaenidae). *Bulletin of the Japanese Society of Scientific Fisheries* **44**: 121-125.

Tamura, K. and Nei, M. (1993). Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution* **10**: 512-526.

Taniguchi, N. (1969a). Comparative osteology of the sciaenid fishes from Japan and its adjacent waters. I. Neurocranium. *Japanese Journal of Ichthyology* **16**: 55-67.

Taniguchi, N. (1969b). Comparative osteology of the sciaenid fishes from Japan and its adjacent waters. II. Vertebrae. *Japanese Journal of Ichthyology* **16**: 153-156.

Taniguchi, N. (1970). Comparative osteology of the sciaenid fishes from Japan and its adjacent waters. III. Premaxillary and dentary. *Japanese Journal of Ichthyology* **17**: 135-140.

Taylor, J.G. and Pearce, A.F. (1999). Ningaloo Reef currents: implications for coral spawn dispersal, zooplankton and whale shark abundance. *Journal of the Royal Society of Western Australia* **82**: 57-65.

Taylor, M.D., Laffan, S.D., Fielder, D.S. and Suthers, I.M. (2006). Key habitat and home range of mulloway *Argyrosomus japonicus* in a south-east Australian estuary: finding the estuarine niche to optimise stocking. *Marine ecology Progress Series* **328**: 237-247.

Temminck, C.J. and Schlegel, H. (1843). Pisces. In: *Fauna Japonica* (de Siebold, P.F., Ed.). Lugduni Batavorum, Batavia.

Templeton, A.R., Crandall, K.A. and Sing, C.F. (1992). A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics* **132**: 619-633.

Thacker, C.E., Thompson, A.R., Roje, D.M. and Shaw, E.Y. (2007). New expansions in old clades: population genetics and phylogeny of *Gnatholepis* species (Teleostei: Gobioidei) in the Pacific. *Marine Biology* **153**: 375-385.

Thomson, J.M. (1959). Some aspects of the ecology of Lake Macquarie, NSW, with regard to an alleged depletion of fish. *Australian Journal of Marine and Freshwater Research* **10**: 375-387.

Tower, R.W. (1908). The production of sound in the drumfishes, the sea-robin and the toadfish. *Annals of the New York Academy of Sciences* **18**: 149-180.

Travers, M.J. (1999). *Comparisons between the fish faunas in sand and seagrass habitats in Shark Bay, Western Australia*. Unpublished Honours Thesis. Murdoch University, Perth.

Trewavas, E. (1964). Sciaenid fishes with a single mental barbell. *Copeia* **1964**: 107-117.

Trewavas, E. (1977). The sciaenid fishes of the Indo-West Pacific. *Transactions of the Royal Society, London* **33**: 253-541.

Tveiten, H., Solevag, S.E. and Johson, H.K. (2001). Holding temperature during the breeding season influences final maturation and egg quality in common wolfish. *Journal of Fish Biology* **58**: 374-385.

Ueng, J.P. and Huang, B.Q. (1998). Circadian rhythm of sound production in Japanese croaker, *Argyrosomus japonicus*. *Journal of the Fisheries Society of Taiwan* **25**: 287-292.

Ueng, J.P., Huang, B.Q. and Mok, H.K. (1999). Ontogenetic changes of sound production in Japanese croaker, *Argyrosomus japonicus* (Sciaenidae). *Journal of the Fisheries Society of Taiwan* **26**: 13-21.

Ueng, J.P., Huang, B.Q. and Mok, H.K. (2007). Sexual differences in the spawning sounds of the Japanese Croaker, *Argyrosomus japonicus* (Sciaenidae). *Zoological Studies* **46**: 103-110.

Valesini, F.J., Clarke, K.R., Eliot, I. and Potter, I.C. (2003). A user-friendly quantitative approach to classifying nearshore marine habitats along a heterogeneous coast. *Estuarine, Coastal and Shelf Science* **57**: 163-177.

von Bertalanffy, L. (1957). Quantitative laws in metabolism and growth. *Quarterly Review of Biology* **32**: 217-231.

Vouglitois, J.J., Able, K.W., Kurtz, R.J. and Tighe, K.A. (1987). Life history and population dynamics of the bay anchovy in New Jersey. *Transactions of the American Fisheries Society* **116**: 141-153.

Walker, D.I. (1990). Seagrass in Shark Bay, Western Australia. In: *Research in Shark Bay, Report of the France-Australe Bicentenary Expedition Committee* (Berry, P.F., Bradshaw, S.D. and Wilson, B.R., Eds). *pp.* 101-106. Western Australian Museum, Perth.

Wallace, J.H. and Schleyer, M.H. (1979). Age determination in two important species of South African angling fishes, the kob (*Argyrosomus hololepidotus* Lacep.) and the spotted grunter (*Pomadasys commerssoni* Lacep.). *Transactions of the Royal Society of South Africa* **44**: 15-26.

Wallace, R.A. and Selman, K. (1981).Cellular and dynamic aspects of oocyte growth in teleosts. *American Zoology* **21**: 325-343.

Walsh, C.T., Pease, B.C. and Booth, D.J. (2003). Sexual dimorphism and gonadal development of the Australian longfinned river eel. *Journal of Fish Biology* **63**: 137-152.

Wang, S., Hard, J.J. and Utter, F. (2002). Salmonid inbreeding: A review. *Reviews in Fish Biology and Fisheries* **11**: 301-319.

Ward, R.D. (2000). Genetics in fisheries management. *Hydrobiologia* **420**: 191-201.

Ward, R.D. and Grewe, P.M. (1994). Appraisal of molecular genetic techniques in fisheries. *Review of Fish Biology and Fisheries* **4**: 300-325.

Ward, R.D., Woodark, M. and Skibinski, D.O.F. (1994). A comparison of genetic diversity levels in marine, freshwater and anadromous fishes. *Journal of Fish Biology* **44**: 213-222.

Ward, R.D., Zemlak, T.S., Innes, B.H., Last, P.R. and Herbert, P.D.N. (2005). DNA barcoding Australia's fish species. *Philosophical Transactions of the Philosophical Society, Series B: Biological Sciences* **360**: 1847-1857.

Watts, R.J. and Johnson, M.S. (2004). Estuaries, lagoons and enclosed embayments: habitats that enhance population subdivision of inshore fishes. *Marine and Freshwater Research* **55**: 641-651.

Weir, B.S. and Cockerman, C.C. (1984). Estimating F-statistics for the analysis of population structure. *Evolution* **38**: 1358-1370.

Wellborn, G.A. (1994). Size-biased predation and prey life histories: a comparative study of freshwater amphipod populations. *Ecology* **75**: 2104-2117.

Wells, F.E. (1980). The distribution of shallow water marine prosobranch gastropod molluscs along the coast of Western Australia. *Veliger* **22**: 232-247.

West, G. (1990). Methods of assessing ovarian development in fishes: a review. *Australian Journal of Marine and Freshwater Research* **41**: 199-222.

West, G.B., Brown, J.H. and Enquist, B.J. (2001). A general model for ontogenetic growth. *Nature* **413**: 628-631.

West, R.J. (1993). *Estuarine fisheries resources of two southeastern Australian rivers*. Unpublished PhD Thesis. University of New South Wales, Sydney.

West, R.J. and Gordon, G.N.G. (1994). Commercial and recreational harvest of fish from two Australian coastal rivers. *Australian Journal of Marine and Freshwater Research* **45**: 1259-1279.

West, R.J. and Walford, T.R. (2000). Estuarine fishes in two large eastern Australian coastal rivers – does prawn trawling influence fish community structure? *Fisheries, Management and Ecology* **7**: 523-536.

West-Eberhard, M.J. (1989). Phenotypic plasticity and the origins of diversity. *Annual Reviews of Ecology and Systematics* **20**: 249-278.

Whitfield, A.K., Paterson, A.W., Bok, A.H. and Kok, H.M. (1994). A comparison of the ichthyofaunas in two permanently open eastern Cape estuaries. *South African Journal of Zoology* **29**: 175-185.

Will, K.W., Mishler, B.D. and Wheeler, Q.D. (2005). The perils of DNA barcoding and the need for integrative taxonomy. *Systematic Biology* **54**: 844-851.

Williams, T. and Bedford, B.C. (1974). The use of otoliths for age determination. In: *The Ageing of Fish* (Bagenal, T.B., Ed.). *pp*. 114-123. Unwin Brothers, Surrey.

Wilson, B.R. and Allen, G.R. (1987). 3. Major components and distribution of marine fauna. In: *Fauna of Australia, 1A General Articles* (Dyne, G.R., Ed.). *pp.* 43-68. Bureau of Flora and Fauna, Canberra.

Wilson, C.A. and Nieland, D.L. (1994). Reproductive biology of red drum, *Sciaenops ocellatus*, from the neritic waters of the northern Gulf of Mexico. *Fishery Bulletin* **92**: 841-850.

Wilson, C.A. and Nieland, D.L. (2001). Age and growth of red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico off Louisiana. *Fishery Bulletin* **99**: 653-664.

Wilson, G. (2004). *Bream, Flathead and Mulloway and how to Catch Them*. Australian Fishing Network, South Croyden.

Winemiller, K.O. and Taylor, D.H. (1982). Inbreeding depression in the convict cichlid, *Cichlasoma nigrofasciatum*. *Journal of Fish Biology* **21**: 399-402.

Winstanley, R.H. (1990). A fisheries manager's application of minimum legal lengths. In: *Minimum legal sizes and their use in fisheries management. Australian Society for Fish Biology workshop proceedings* (Hancock, D.A., Ed.). *pp*. 51-56. Australian Government Publishing Services, Canberra.

Wishart, D.S., Stothard, P. and van Domselaar, G.H. (2000). PepTool and GeneTool: platform-independent tools for biological sequence analysis. *Methods in Molecular Biology* **132**: 93-113.

Wolff, W.J. (2000a). Causes of Extirpations in the Wadden Sea, an estuarine area in The Netherlands. *Conservation Biology* **14**: 876-885.

Wolff, W.J. (2000b). The south-eastern North Sea: losses of vertebrate fauna during the past 2000 years. *Biological Conservation* **95**: 209-217.

Woo, M., Pattiaratchi, C. and Schroeder, W. (2006). Summer surface circulation along the Gascoyne continental shelf, Western Australia. *Continental Shelf Research* **26**: 132-152.

Wright, P.J. (1991). The influence of metabolic rate on otolith increment width in Atlantic salmon parr, *Salmo salar* L. *Journal of Fish Biology* **38**: 929-933.

Wright, P.J., Talbot, C. and Thorpe, J.E. (1992). Otolith calcification in Atlantic salmon parr, *Salmo salar*, and its relation to photoperiod and calcium metabolism. *Journal of Fish Biology* **40**: 779-790.

Yamaguchi, A., Todoroki, T. and Kume, G. (2006). Reproductive cycle, sexual maturity and diel-reproductive periodicity of white croaker, *Pennahia argentata* (Sciaenidae), in Ariake Sound, Japan. *Fisheries Research* **82**: 95-100.

Yearsley, G.K., Last, P.R. and Ward, R.D. (2001). *Australian seafood handbook. An identification guide to domestic species.* CSIRO Marine Research and Fisheries Research and Development Corporation.

Yearsley, G.K., Last, P.R. and Hoese, D.F. (Eds) (2006). *Standard names of Australian fishes.* CSIRO Marine and Atmospheric Research Paper 009. CSIRO Marine and Atmospheric Research, Hobart.

Young, G.C. and Potter, I.C. (2002). Influence of exceptionally high salinities, marked variations in freshwater discharge and opening of estuary mouth on the characteristics of a normally-closed estuary. *Estuarine, Coastal and Shelf Science* **55**(2): 223-246.